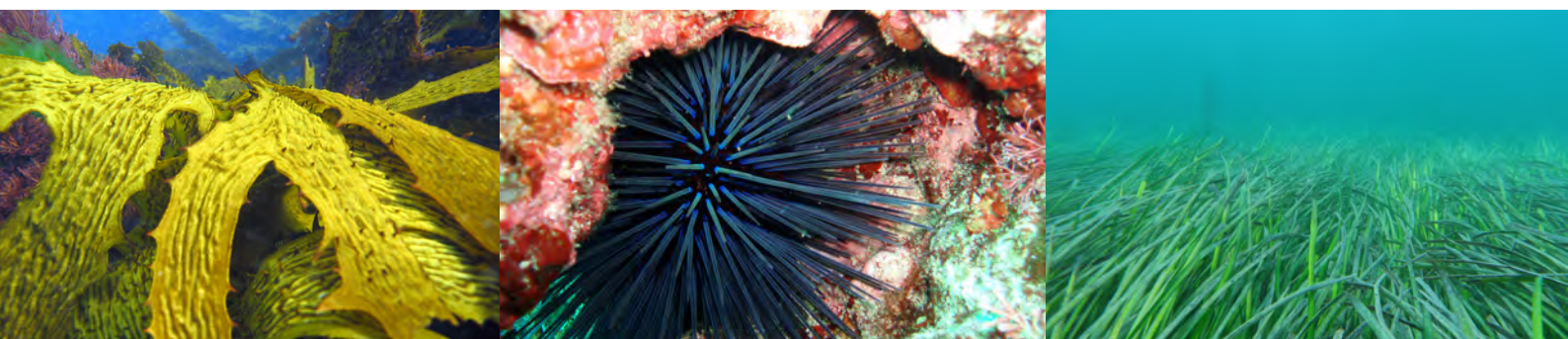


Trophic effects through herbivory at Ningaloo Reef

Final report for WAMSI Node 3.2: Biodiversity assessment, ecosystem impacts of human usage

Adriana Vergès, Glenn Hyndes and Mathew Vanderklift

CMER 2011-01



This report has been prepared to summarise the findings and management implications of WAMSI Node 3: Project 3.2: Biodiversity assessment, ecosystem impacts of human usage and management strategy evaluation: Trophic effects through herbivory at Ningaloo Reef.

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Trophic effects through herbivory at Ningaloo Reef.

Final report for WAMSI Node 3.2: Biodiversity assessment, ecosystem impacts of human usage and management evaluation.

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Executive Summary

The Ningaloo Marine Park (NMP) is a fringing coral-reef system that encompasses approximately 263,343 ha along the Pilbarra coast of Western Australia. It was gazetted in 1987 and a revised Management Plan was approved in 2005. The management plan identified the diversity of fish found within the Ningaloo Marine Park as a key ecological value, and fishing (particularly recreational) as a major pressure on this value. As a consequence, the management plan established an objective to “ensure the species distribution and abundance of finfish species are not unacceptably impacted by recreational and commercial fishing”. A spatial management strategy has been established using range of management zones, including sanctuary zones, to achieve this objective. To inform management of the park, a large research programme was established within the Western Australian Marine Science Institute (WAMSI). The current study was nested in “Project 3.2: Biodiversity assessment, ecosystem impacts of human usage and management strategy evaluation” of WAMSI Node 3.

Coral reefs are diverse ecosystems which host abundant populations of consumers and algae in spatial mosaics of both coral and algal dominated habitats. A key ecological process in coral-reef ecosystems is herbivory, which has direct effects on macroalgae and indirect effects on corals by influencing the outcome of coral-algal competition. Despite high diversity and abundance of nominally herbivorous fish, recent studies indicate that only a small subset of taxa are capable of removing dominant macroalgae once these become established. This limited functional redundancy highlights the potential vulnerability of coral reefs to disturbance and stresses the need to assess the functional role of individual species of herbivores.

This study was nested in sub-project 3.2.2 “Ecosystem impacts of human usage and the effectiveness of zoning for the biodiversity conservation” in Node 3.2. The focus of this study was on trophic effects in the NMP. Due to the importance of herbivores in coral-reef systems, this study focused on characterising and quantifying the process of herbivory in the NMP with a particular emphasis on the removal of adult macroalgae.

We used a range of approaches to gain an understanding of spatial and species-related patterns in herbivory in five distinct studies. Using underwater video cameras and *Sargassum myriocystum* assays, 23 different fish species were observed consuming macroalgae, but seven species (*Naso unicornis*, *Kyphosus* sp., *K. vaigiensis*, *Siganus doliatus*, *Scarus ghobban*, *S. schlegeli* and initial-phase *Scarus* sp.) together accounted for 95% of the observed bites across five regions. Of these species, three were identified as the most important in consuming macroalgae: *N. unicornis*, *Kyphosus* sp. and *K. vaigiensis*. These results were supported by stable isotope analyses that incorporate nutrients from food sources over far longer periods than those examined using the assay approach.

We quantified spatial patterns of macroalgal consumption and food sources across a range of scales. Firstly, across reef habitats separated by hundreds of meters, herbivory was always greatest in the structurally complex coral-dominated outer reef and reef flat habitats, which are also characterised by the highest biomass of herbivorous fish. Secondly, we showed a high degree of variability in grazing rates among regions separated by 100s km in the marine park, with different species responsible for macroalgal removal among those regions. Either *N. unicornis* or *Kyphosus* spp. were responsible for the majority of the grazing. Thirdly, we showed variability in the importance of different food sources across both habitats and regions for some consumers (e.g. *Siganus* spp.) but consistency for other species (e.g. *Naso unicornis*, *Kyphosus* spp.), which is likely to reflect shifts in food source availability or feeding preferences. Lastly, we found strong transcontinental differences between Keppel Islands in the Great Barrier Reef (GBR) on the east coast of Australia and Ningaloo Reef in both the diversity of the species observed feeding and on the species

composition of the roving herbivorous fish community. In Ningaloo Reef, 23 species were observed biting on *Sargassum*, compared with just 8 in the Keppel Islands. *Sargassum* consumption in the Keppel Islands was dominated by a small number of species and supports the identification of *Naso unicornis* as a key browser species. The larger number of species feeding on macroalgae in Ningaloo Reef suggests that there may be higher functional redundancy among macroalgal consumers in this system.

We also characterised the benthic community dynamics of the reef-flat and lagoon habitats to identify seasonal patterns and we experimentally determined the importance of herbivory on algae recruitment in these two habitats. Differences among habitats in algal biomass were strongly influenced by season. Lagoon habitats only had higher biomass than reef-flat habitats during part of the year (late summer/ early autumn). Herbivory had an equally strong effect on the community composition of algal recruits in the lagoon and reef flat habitats, despite the reef flat hosting a herbivorous fish community that was an order of magnitude greater in terms of biomass than the lagoon, which is characterised by younger and smaller fish (e.g. *Scarus* initial phase).

Management implications and recommendations are:

- We have provided a baseline survey of all nominally herbivorous fish species (fish density and quantitative feeding activity data) across a range of regions and we have identified key species that should be closely monitored.
- We provide evidence that structural complexity is a key factor influencing herbivory. Conservation efforts should thus focus on conserving this trait (e.g. protect coral habitats from anchoring damage).
- Although herbivorous fishes are not presently targeted by fishers in NMP, this trophic group is increasingly being targeted for exploitation elsewhere. We have provided quantitative data that can be used to support potential management plans aimed at protecting herbivorous fishes from disturbances on the basis of their critical role for promoting coral-reef resilience.
- A direct comparison of herbivory between different coral-reef systems indicates that Ningaloo Reef is a comparatively pristine system.
- Variability in grazing rates across NMP, and the species responsible for grazing, indicates that any future monitoring of key species needs to take place over different regions of the marine park.
- Herbivory is a dominant mechanism that influences the abundance of fleshy macroalgae when recruitment space is equal in the lagoon and reef-flat habitats. Zoning needs to account for the movement of key herbivores across habitats when determining boundaries of management zones.
- Monitoring the biomass of *Naso unicornis*, *Kyphosus* spp. inside and outside sanctuary zones will provide crucial information of the potential influence of zoning on macroalgal removal in the NMP, as well as a region's ability to recover from disturbances that enhance macroalgal production.
- Quantitative data on rates of herbivory from our studies can be incorporated into broad-scale fish density data from other projects to model the effects of disturbances and changes in management strategies on herbivory, and potential effects to the system as a whole.
- Data on the spatial patterns of movement are needed for all key macroalgal grazers to ensure that sanctuary zones preserve their abundances.
- Research is needed to further investigate the potential for indirect ecological effects and trophic cascades through the removal of higher order predators (e.g. sharks) in the NMP.

CHAPTER 1. Background

Ningaloo Marine Park and WAMSI

The Ningaloo Marine Park, encompassing approximately 263,343 ha, was gazetted in 1987 and a revised Management Plan was approved in 2005. The management plan identified the diversity of fish found within the Ningaloo Marine Park as a key ecological value, and fishing (particularly recreational) as a major pressure on this value. As a consequence, the management plan established an objective to “ensure the species distribution and abundance of finfish species are not unacceptably impacted by recreational and commercial fishing”. The primary strategy to achieve this objective was to establish a range of management zones within the marine park, including sanctuary zones where fishing activities are excluded.

A large research programme was established at Ningaloo Marine Park as part of “Node 3: Conserving Marine Biodiversity” of the Western Australian Marine Science Institute (WAMSI). This Node was established to gain a better understanding of issues including the effect of climate change, fisheries, tourism, coastal development and industry on the marine biodiversity and social values of the Ningaloo Marine Park. A range of sub-projects were nested in “Project 3.2: Biodiversity assessment, ecosystem impacts of human usage and management strategy evaluation” of WAMSI Node 3:

- 3.2.1 Diversity, abundance and habitat utilisation of sharks and rays;
- 3.2.2 Ecosystem impacts of human usage and the effectiveness of zoning for the biodiversity conservation;
- 3.3.3 Management strategy evaluation; and
- 3.3.4 Ningaloo Research program start-up project for impacts of human usage, oceanography and management strategy evaluation.

This study was nested in “3.2.2 Ecosystem impacts of human usage and the effectiveness of zoning for the biodiversity conservation”. The focus of this study was on the trophodynamics and trophic effects in the Ningaloo Marine Park. Due to the importance of herbivores in coral-reef systems (see below) this study focused on gaining an understanding of the role of herbivores in maintaining the balance between corals and macroalgae in this coral-reef system.

Trophic effects in coral-reef systems

Herbivory is a key ecological process in coral reefs that is considered fundamental to the balance between corals and macroalgae. A diverse herbivorous community is thought to strongly influence the resilience of coral reefs, i.e. their ability to reorganise and maintain ecosystem function following disturbance (Bellwood et al. 2004; Mumby et al. 2006). Indeed, overfishing of roving herbivorous fishes is considered a major factor contributing to reef degradation. This is often linked to phase shifts from coral to macroalgal dominance

(Hughes 1994; McClanahan et al. 2001; Graham et al. 2006). It is therefore crucial to understand the role that roving herbivorous fishes play in maintaining that balance between macroalgae and coral. In gaining that understanding, it is important to note that roving herbivorous fishes have recently been shown to exhibit widely varying feeding modes and diets (Choat et al. 2002; Choat et al. 2004; Crossman et al. 2005), rather than conforming to a uniform functional group (Bellwood et al. 2004; Green and Bellwood 2009; Hoey and Bellwood 2010). It is crucial, therefore, to gain an understanding the varying roles of these herbivores in coral-reef systems for effective management of these systems.

Need

Understanding key ecological processes in marine landscapes is fundamental to effective marine management, particularly when management utilises spatial strategies such as marine protected areas (MPAs). MPAs are a management tool used in numerous countries for a variety of objectives (Halpern 2003). Marine parks form a major management tool for management of the marine environment by the Department of Environment and Conservation in Western Australia. Like many marine parks in Western Australia, the Ningaloo Marine Park was established to maintain biodiversity and ecological integrity through a multiple-use spatial management system. The establishment of zones designated for different levels of use allows for the continued use of the area, but provides a higher level of protection than would otherwise be the case.

As stated above, herbivores play a critical role in the resilience of coral-reef systems, yet they are exposed to human impacts. Despite their importance, very little is known about the roles of different types of herbivorous fish and invertebrates in the Ningaloo Marine Park. The vast majority of work on roving herbivorous fishes has taken place in the Great Barrier Reef on the east coast of Australia, or in the Caribbean Sea. Thus, there is a need to gain an understanding of the key species responsible for the removal of macroalgae in the Ningaloo Marine Park. Together with other WAMSI Node 3.2 studies examining fish distributions inside and outside sanctuary zones, as well as movement patterns in the marine park, an understanding of herbivory will provide the basis for an assessment of any shifts in herbivory associated with changed zoning within the marine park.

Report structure

The broad aim of this study was to gain an understanding of the trophic effects of herbivores and their varying roles in the Ningaloo Marine Park. We also aimed to determine the variability in the consumption of food sources at different spatial scales throughout the park, providing critical information for spatial management. The report will provide the results of a range of studies related to herbivory using multiple descriptive and experimental approaches. The results of each discrete study are presented as individual chapters, each providing an introduction, methods, results, discussion and conclusion, as outlined below:

1. Spatial patterns in herbivory on a coral reef are influenced by structural complexity but not by algal traits.
2. Herbivore diversity on coral reefs: a transcontinental comparison.
3. Variation in macroalgal herbivory by fishes across a western-continental coral-reef system.
4. Variability in the food sources of herbivorous invertebrates and fishes in a coral-reef system: a stable isotope approach.
5. The role of herbivory on the spatial distribution of recruiting and established algal communities in coral versus algal dominated habitats.

All but Study 2 focused entirely on herbivory patterns and processes at Ningaloo Reef. We were provided with an opportunity to collaborate with researchers at James Cook University to carry out a comparative study (Study 2) on herbivory rates between Ningaloo Reef and GBR. This allowed us to place herbivory rates in the context of another large coral-reef system, and provided us with the technical skills to examine the regional patterns in herbivory at Ningaloo Reef (Study 3).

Finally, the report provides a synthesis of the conclusions from each chapter and discusses the implications of our findings to marine management in the region.

CHAPTER 2. Spatial patterns in herbivory on a coral reef are influenced by structural complexity but not by algal traits

Adriana Vergés, Mathew A. Vanderklift, Christopher Doropoulos, Glenn A. Hyndes

Introduction

Spatial heterogeneity in ecosystems can strongly influence population structure, community composition and ecosystem processes (Pickett & Cadenasso 1995). Herbivory can generate spatial heterogeneity by regulating rates of primary production and nutrient cycling (Augustine & McNaughton 1998, Augustine & Frank 2001), modifying plant community composition, diversity and biomass (Milchunas & Lauenroth 1993, Hulme 1996), and/or directly disturbing habitats physically (e.g. through burrowing; (Huntly & Inouye 1988, Knapp et al. 1999)). Several factors are known to control the spatial distribution of herbivory, including abiotic influences such as topography or distance to water (in terrestrial systems), and biotic influences such as plant distribution, nutritional quality, predation, herbivore social behaviour (e.g. herding), and human management practices (Coughenour 1991, Bailey et al. 1996, Adler et al. 2001, Ogutu et al. 2010). Additionally, feedback mechanisms between herbivory and plant quality can also influence spatial patterns of herbivory. For example, while herbivory generally decreases plant biomass, it often enhances nutrient recycling and availability (McNaughton et al. 1997, Augustine et al. 2003), although these short-term positive feedbacks may eventually result in a compositional shift towards less palatable plant species (Pastor et al. 1993). However, much of this knowledge comes from wildlife and rangeland management literature that deals mostly with large ungulates, and we know comparatively less about what controls spatial patterns of herbivory in ecosystems characterised by other consumers.

This study focuses on the processes that control the spatial distribution of herbivory in coral reefs, ecosystems that are characterised by some of the highest rates of herbivory (Hay 1991, Hay & Steinberg 1992, Augustine & Frank 2001). Herbivores can remove over 90% of daily algal production in shallow coral reefs (Hatcher & Larkum 1983, Carpenter 1988, Augustine & Frank 2001), and the presence of abundant coral depends on high levels of herbivory (Lewis 1986, Burkepile & Hay 2006, Hughes et al. 2007). Indeed, herbivorous fish play a crucial role in maintaining coral-reef resilience (i.e. the ability of a system to absorb disturbances whilst maintaining ecosystem function (Holling 1973)) by consuming macroalgae that can otherwise outcompete corals when new space becomes available following disturbance (Hughes 1994, McClanahan et al. 2001, McCook et al. 2001, Diaz-Pulido & McCook 2003, Mumby et al. 2006). However, the impact of herbivores is usually not uniform across all habitats, and coral reefs may be viewed as spatial mosaics of animal- and macroalgae-dominated communities characterised by different intensities of herbivory (Hay 1981a, Lewis & Wainwright 1985, Lewis 1986, Fox & Bellwood 2007). Thus, variations in the intensity of herbivory between different parts of a reef separated by short distances (tens to hundreds of meters) can be greater than differences among reefs that are many kilometres apart (Russ 1984). Despite the existence of such marked spatial patterns in herbivory in coral reefs, we have a limited knowledge of the factors that drive differences across reef gradients.

Early studies dealing with spatial patterns in coral reefs focused on the distribution of marine plants, and highlighted the importance of herbivory for maintaining differences among habitats (Hay 1981a, Hatcher & Larkum 1983, Hay et al. 1983a, Lewis 1986, McCook 1997). Other studies focused on the distribution of herbivores in different sections of the reef and found marked variations in densities and species composition (Russ 1984, Lewis & Wainwright 1985, Fox & Bellwood 2007, Wismer et al. 2009). Several mechanisms involving

both abiotic and biotic influences have been proposed to explain the striking gradients in the intensity of herbivory observed on coral reefs worldwide. Among the abiotic influences, wave exposure and depth are considered to inhibit herbivory. Herbivory is often lowest in the first 1-2 meters of water, where turbulence associated with wave impact hinders the feeding ability of fish, it is greatest a few meters below the surface, and decreases at greater depths (> 20m) (Hay 1981b, Vergés et al. 2009, Brokovich et al. 2010). In contrast, structural complexity and availability of refuges are considered to enhance herbivory (Hay 1981b, Hay et al. 1983a, Lewis & Wainwright 1985, McCook 1997). In terms of biotic factors, large grazers appear to aggregate in zones of high algal turf production, although the mechanisms by which fish respond to productivity are not clear (Russ 2003). Despite many such hypotheses having been invoked to explain spatial variation of herbivory in coral reefs, few studies have experimentally tested the importance of specific mechanisms. Moreover, herbivory in coral reefs is a process that involves a wide range of consumers with highly variable feeding modes and diets and with contrasting ecological functions (Choat 1991), and there is a need to quantify and assess the impact of different functional groups separately. For example, differences in turf algae productivity may influence (and be influenced by) the distribution of fishes that consume turf algae (Russ 2003), but probably have no effect on species that feed on macroalgae.

Roving herbivorous fishes have been clearly identified as the key herbivores in undisturbed coral reefs (Hughes et al. 2007). However, they do not constitute an ecologically uniform group, but can be broadly classified into grazer and browser functional groups, depending on their diet and mode of feeding (Bellwood et al. 2004, Hoey & Bellwood 2010a). Grazing taxa (including scraping and excavating parrotfishes) typically feed on the epilithic algal matrix (EAM *sensu* Wilson (Wilson et al. 2003)) and on crustose coralline algae, and constitute the majority of herbivorous fishes on coral reefs. In contrast, only a handful of species are considered to be browsers – that is, species that consume large erect macroalgae (Bellwood et al. 2006a, Fox & Bellwood 2008, Hoey & Bellwood 2009, Bennett & Bellwood 2011). Grazers and browsers are thought to play distinct and complementary roles in avoiding phase shifts towards macroalgal dominance (Bellwood et al. 2004, Bellwood et al. 2006a). Grazers can preclude an increase in overall algal biomass, prevent macroalgal growth by consuming macroalgal recruits, and provide space for coral recruitment, while browsers consume the adult brown seaweeds that typically dominate coral reefs in the absence of herbivory, and therefore have the potential to reverse phase shifts once macroalgae are established in reefs (Bellwood et al. 2004, Bellwood et al. 2006a). Recent studies have highlighted the importance of macroalgal consumption and have identified the key species or functional groups responsible for this ecological function (Bellwood et al. 2006a, Fox & Bellwood 2007, Hoey & Bellwood 2009, Cheal et al. 2010, Bennett & Bellwood 2011), but we know little about the mechanisms that control the distribution and abundance of these browsers.

In this study, we quantified spatial patterns of macroalgal herbivory by fishes across a coral reef, tested for similar spatial patterns in potential explanatory variables, and then used manipulative and mensurative experiments to test some hypotheses arising from the patterns observed. We tested for the presence of spatial variation in herbivory by quantifying consumption of erect macroalgae and measuring the biomass and composition of herbivorous fishes among a cross section of a coral reef (lagoon, reef flat and outer reef habitats). We then related patterns in herbivory to the spatial distribution of algal cover, algal biomass and structural complexity in these three habitats. In the manipulative and mensurative experiments, we selected two habitats with contrasting levels of herbivory (reef flat and lagoon) and used herbivore exclusion and feeding experiments to test hypotheses about the mechanisms that might cause the observed consumption patterns. In particular, we asked: (1) Does consumption of macroalgae relate to spatial patterns in macroalgal productivity, nutritional quality, community composition and/or palatability? (2) Does herbivory influence macroalgal nutritional quality? and (3) Does benthic structural complexity and proximity to reef influence the distribution of macroalgal herbivory.?

Materials and Methods

Study area

This study was conducted at Ningaloo Reef (Western Australia), a fringing reef approximately 290 km in length. Ningaloo Reef is an arid-zone reef where extensive coral reefs occurs in close proximity to the mainland. The study was conducted between April 2008 and September 2009 in the Mandu (22° 06' S, 113° 52' E) and Maud (23° 07' S, 113° 44' E) sanctuary zones of the Ningaloo Marine Park. At Ningaloo, the reef crest is narrow and mostly devoid of coral growth, the reef flat landward of the reef crest hosts coral communities across a width of approximately 150 m, and the outer reef slopes seaward of the reef crest presenting a well-developed spur and groove morphology to depths of 30 m (Cassata & Collins 2008) (Digital Appendix Fig 1). In the Mandu sanctuary zone, the reef encloses a lagoon that is about 1 km in width. In the Maud sanctuary zone, the width of the lagoon ranges more widely from 1.7 km to 7 km. In each location, the lagoon is populated with sparse corals, sandy substrata and patches of macroalgae. The tides in the area have a maximum ~ 2 m range at spring tides.

Most of this study took place in the Mandu sanctuary zone, where we haphazardly selected three study sites in each of three habitats that characterise the area: lagoon, reef flat and outer reef (Digital Appendix Fig. 1). We performed one experiment (on the effects of reef proximity on macroalgal removal) in the Maud sanctuary zone, where we haphazardly selected three study sites at the boundary between the reef flat and lagoon, with each site located about 250 m apart.

Patterns in rates of consumption of macroalgae among habitats

Relative differences in consumption of erect macroalgae between lagoon, reef flat and outer reef habitats at all Mandu sites were measured in April 2008 using tethered pieces of *Sargassum myriocystum*. This brown alga is rapidly eaten (within hours) and has a relatively simple morphology, which allowed us to estimate biomass loss from differences in length before and after deployment. *S. myriocystum* plants bear 3 – 6 main lateral branches per individual, and each of these has a consistent length-weight relationship (148.01 ± 9.241 mg/cm). Patterns of herbivory were determined by placing lateral branches of *S. myriocystum* of 15 cm in length and similar weight (mean 2.13 ± 0.19 g; $n = 26$) in three sites at each of the lagoon, reef flat and outer reef habitats. In each site, *S. myriocystum* lateral branches ($n=25$) were distributed haphazardly and tethered to the available substrata using cable ties. In the lagoon habitat, branches were either tethered to other macroalgae or to loose pieces of dead coral on the sand at around 1.5 m depth. In the reef flat habitat, branches were mostly tethered to pieces of dead coral covered in epilithic algal matrix adjacent to live corals, at 1-2 m depth. In the outer reef habitat, branches were mostly tethered to coral pieces and crustose coralline rocky surfaces at about 6 m depth – the shallowest depth that we could easily access in regular swell conditions. Tethered algae were collected 4-7 hours after deployment, and mass consumed was estimated from the total length consumed, and converted to mass consumed per hour. Some tethered algae became detached and lost, leading to an unbalanced data set (final n ranged from 17 to 25 depending on site). Replicates where algae became wholly detached were not included in the analysis because we could not be sure that detachment was due to herbivory.

Patterns in biomass and species composition of herbivorous fish among habitats

Censuses of the herbivorous fish assemblage were carried out during a two-week period in November 2008 at three sites in each of the three habitats in the Mandu Sanctuary zone (Fig 2.1). Fishes were counted along eight 25 x 5 m haphazardly placed transects per site during daylight hours (avoiding 2 hours after sunrise and before sunset). Fish counts were performed swimming at a constant speed (ca. 8 minutes per 25 m transect) and counting and estimating the size of fish within 2.5 m of either side of the transect line. Fishes were identified to species level and their total length was estimated in 5 cm size categories. Size estimates were validated using objects of known length. Length estimates for individual fish were converted to biomass using the allometric length-weight conversion $W = a * TL^b$, where W is weight in grams, TL is total length and parameters a and b are constants obtained from the literature (Froese & Pauly 2005). We restricted our counts to mobile herbivorous and 'nominally' herbivorous fishes, excluding pomacentrids (Choat et al. 2002). We identified 25 species from the families Acanthuridae, Siganidae, Kyphosidae and Labridae (parrotfishes). These data were analysed in two ways: one including all species of roving herbivorous fish and one including only species that are considered to be browsers (consumers of macroalgae). Of the species recorded, 11 taxa were identified as browsers of erect macroalgae based on gut content analyses (Westera 2003) and direct observations on remote video cameras (unpubl. data): *Kyphosus vaigiensis*, *Naso lituratus*, *Naso* spp., *Naso unicornis*, *Scarus ghobban*, *S. schlegeli*, initial-phase *Scarus* sp., *Siganus argenteus*, *S. doliatus*, and *S. trispilos*.

Patterns in cover, biomass and species composition of macroalgae among habitats

To determine whether spatial patterns in macroalgal herbivory were related to macroalgal distribution, we measured algal cover and algal biomass and community composition at each site at Mandu in November 2008. Algal cover was quantified using the line intercept benthic survey method described by Fox and Bellwood (Fox & Bellwood 2007). We conducted a total of 6 replicate transects (total of 30 points per replicate) in each of the habitats at the three sites.

Macroalgal biomass and community composition were measured by clearing three 0.25 m² haphazardly placed quadrats of all macroalgae (arbitrarily defined as algae with thallus larger than 1 cm) at each site. Algal samples were bagged and returned to the laboratory, where they were sorted to genus level (where possible) and weighed. Algal taxa that we were unable to identify were classified according to broad functional groups (brown, green or red; filamentous, encrusting or foliose).

Patterns in coral cover and structural complexity

To determine whether patterns in consumption of macroalgae were related to topographic complexity, we measured coral cover (which provides three-dimensional structure and potential refuges) and estimated a rugosity ratio ($n = 3$) at each site. Live coral cover was quantified using the line intercept benthic survey method described above for algal cover. To measure rugosity, a 10 m light chain was placed along the substrate contour, and the equivalent straight line horizontal distance encompassed by the 10 m of chain was measured ($n = 3$). The rugosity ratio (R) was calculated as the straight line horizontal distance along the reef divided by the total chain length, with values close to unity indicating a flat substratum and lower values indicating a structured habitat (McClanahan & Shafir 1990).

Experimental test of effects of habitat and herbivory on algal consumption, productivity and chemical composition

A transplant experiment was set up to determine the effects of habitat on the consumption and growth of algae and to assess the interactive effects of habitat and herbivory on algal chemical traits. The experiment took place over 6 weeks from April to May 2008 in the Mandu sanctuary zone. Specimens of *Lobophora variegata* (ruffled morphotype, *sensu* Coen and Tanner (Coen & Tanner 1989)) were randomly collected from a lagoon location and placed on reef flat and lagoon habitats under caged and uncaged conditions. This species was chosen because it is commonly found in all coral-reef habitats and because preliminary feeding trials showed it was consumed at a lower rate than other macroalgae (unpubl. data), thus making it more suitable for long-term transplant experiments than other species that are consumed within hours when placed in the reef flat. Three *L. variegata* thalli were placed within each plot. All plots were randomly distributed and placed about 3-5 m apart from each other.

We used triangular cages of 1082 cm² (equilateral triangle with sides of 50 cm and 50 cm in height). Open (uncaged) plots were marked with steel reinforcing bar along the corners. In caged plots, fences and roofs were made with plastic-coated metal mesh (2.5 cm mesh size), thereby excluding large herbivorous fish. Partial cages consisted of steel reinforcing bar marks along the corners with one fenced side and a roof, and were used to control for cage artefacts. All plots had a base of plastic coated mesh to which thalli were attached. The experiment ran for 6 weeks, and the cages were cleaned of fouling organisms once after 2 weeks, although these were not abundant. We recorded blotted wet-weight of algae ($n = 3$) at the beginning and at the end of the experiment and calculated biomass change.

At the end of the experiment, algal thalli were freeze-dried and ground. Nitrogen and carbon content of individual thalli were analysed using a Europa Scientific ANCA-NT 20-20 mass spectrometer. Where possible, *L. variegata* sections of intermediate age (i.e. equidistant from holdfast and thallus edge) were used in the chemical analyses, and care was taken to gently remove any epibiota. Some thalli were so heavily grazed that we used the entire thallus in the analysis, and in some instances we did not have enough mass to conduct chemical analyses, leading to an unbalanced data set.

Experimental test of palatability of algae from high and low herbivory habitats

We compared the palatability and chemical composition of *L. variegata* from high and low herbivory habitats (reef flat and lagoon, respectively) with an experiment performed in April 2008 in the Mandu sanctuary zone. Lagoon and reef flat habitats are characterised by hosting different morphotypes of *L. variegata*. As in other coral-reef ecosystems, an erect ruffled form (hereafter referred to as 'lagoon' morphotype) is usually found on sandy substrata where herbivores are less abundant, whereas the flat decumbent form (hereafter referred to as 'reef flat' morphotype) is usually found underneath coral plates in coral-dominated habitat where herbivores are often more common (Coen & Tanner 1989). The lagoon and reef flat morphotypes of *L. variegata* were offered in pairs of similar initial area in the reef-flat habitat, and replicate pairs ($n = 15$) were at least 3 metres apart from each other. An equal number of controls ($n = 15$) were individually protected from herbivores with plastic window-screen mesh cages (3 mm mesh size). *L. variegata* pairs were left in the field for five days. Replicates with one or two wholly detached algae were not included in the analysis because we could not guarantee that detachment was due to herbivory. Photographs of each algal specimen were taken at the beginning and at the end of the experiment and consumption was measured as changes in area determined using ImageJ analysis software. Five additional thalli of each morphotype were collected at the beginning of the experiment for carbon, nitrogen and phenolic chemical analyses to further identify potential differences in

nutritional traits between habitats. Total phenolic content was quantified spectrophotometrically using a modified Folin-Ciocalteu assay (Bolser et al. 1998).

Effect of proximity to reef on consumption of macroalgae

To test the effects of proximity to reef on macroalgal removal, we tethered *Sargassum myriocystum* lateral branches at a range of distances from the reef flat/ lagoon boundary and measured the amount of algae consumed after 48 hours. We predicted that if structural complexity positively influences herbivory, the rates of macroalgal removal would be higher near the structurally complex reef flat habitat than in flat lagoon habitat. This experiment was performed in the Maud sanctuary zone. We were unable to perform this experiment in the Mandu sanctuary zone because the reef flat/lagoon boundary in that part of the Ningaloo reef is diffuse, with isolated coral heads scattered irregularly near the boundary. In contrast, the reef flat and lagoon habitats are clearly defined at Maud. These two sanctuary zones have similar rates of macroalgal removal and a similar herbivorous fish assemblage (Michael et al., unpublished data). *Sargassum myriocystum* ($n = 3$) lateral branches of about 40 cm in length were tethered at 9 distances relative to the reef flat/ lagoon boundary (-25, 0, 5, 10, 15, 25, 30, 50 and 75 m) at each of three separate sites. Replicates within each distance per site were approximately 15 m apart and parallel to the reef flat/lagoon boundary, and sites were approximately 250 m apart. The length of each individual *S. myriocystum* lateral branch was measured at the beginning and at the end of the experimental period. Since sand was the most common substrate away from the reef, *S. myriocystum* lateral branches were tethered to loose pieces of dead coral that were buried in the sand.

Statistical analyses

All data were checked for normality and equality of variances by visual inspection of scatterplots and distribution of residuals (Quinn & Keough 2002). Where appropriate, data were transformed to conform to parametric assumptions. When assumptions of normality could not be met, the significance of effects was assessed by permutation (McArdle & Anderson 2001).

Patterns in consumption of tethered algae, total fish biomass, coral cover and in the species composition of herbivorous fish and algae communities were analysed using PERMANOVA testing for differences between sites (3 levels, random factor) and habitats (3 levels, fixed factor). Patterns in the cover and biomass of macroalgae and in rugosity were analysed using analysis of variance (ANOVA) with the same design. When significant differences were detected between main effects in ANOVA, Student-Newman-Keuls (SNK) tests were used to resolve the differences among means.

Bray-Curtis distance was our metric in all multivariate analyses and data were fourth-root transformed prior to analyses to reduce the effects of numerically large values (i.e. abundant schooling species) (Clarke 1993). Multivariate differences of fish and algae communities between sites and habitats were visualised using CAP. This procedure produces a constrained ordination and presents data on the axes chosen to best distinguish groups in the data (Anderson & Willis 2003). CAP also provides misclassification errors by carrying out a leave-one-out allocation of observations to groups (habitats), thus indicating the robustness of the classification. In addition, species with the highest contribution to differences among habitats were identified as those that had the highest absolute Pearson correlation with the canonical axis from the CAP analysis. A correlation of $r > 0.4$ was used as an arbitrary cut-off to display potential relationships between individual species and the canonical axes.

We used regressions to determine whether rates of herbivory matched patterns in algal cover, algal biomass and rugosity, and to assess the relationship between herbivory rates and roving herbivorous and browser fish biomass. All data were averaged at the site level.

Linear, polynomial and logarithmic regressions were fitted to the data, and the significant regression that best-fit the data was selected using Akaike's Information Criterion.

In the herbivore exclusion x habitat experiment, changes in biomass and chemical composition in *L. variegata* after 6 weeks were analysed using a four-way ANOVA, testing for differences among sites (3 levels, random), habitats (2 levels, fixed), large herbivore-exclusion treatments (termed 'herbivory effect' throughout; 3 levels, fixed) and plots (3 levels, random and nested in the interaction of Site x Habitat x Herbivory). Differences in feeding between lagoon and reef flat *L. variegata* were analysed using a t-test as outlined by Peterson and Renaud (Peterson & Renaud 1989) to adequately incorporate controls for mass changes not due to consumption. The t-statistic was calculated by comparing the between-plot differences in loss of mass of treatments (Choice 1 – Choice 2, with herbivores) with the between-plot differences in loss of mass of control replicates (Choice 1 – Choice 2, without herbivores). Differences in macroalgal chemical traits between morphotypes were analysed using two-sample t-test when variances were homogenous or Welch's t-test otherwise. Confidence intervals (CI) at 95% of t-test results are presented to assess the validity of non-significant results following Colegrave and Ruxton (Colegrave & Ruxton 2003). The effects of proximity to reef on macroalgal removal were analysed using a two-way ANOVA testing for differences among sites (3 levels, random) and distances (9 levels, fixed).

All PERMANOVA and multivariate analyses were performed using Primer-E v6 software (Clarke & Gorley 2006) with the PERMANOVA+ add-on package (version 1.0.1; (Anderson et al. 2008a)). All ANOVAs were performed using the statistical package GMAV5 (coded by A. J. Underwood and M. G. Chapman, University of Sydney, Australia). T-tests and regression analyses were performed using R software (Version 2.9.0) (Team 2009).

Results

Seascape patterns in the distribution of herbivory, herbivores, macroalgae, coral cover and rugosity

There was a significant difference in the rates of herbivory (measured as consumption of tethered *Sargassum*) among habitats, a pattern that was constant at all sites (Fig 2.1, Table 2.1). No consumption was recorded in the lagoon, whereas in the reef flat and outer reef habitats we found similar rates of about 1-2 cm h⁻¹ (permutational analysis of variance (PERMANOVA) pair-wise tests: Lagoon < Reef flat = Outer reef; $p < 0.02$). Since *Sargassum* was much more abundant in the lagoon than in other habitats (see below), and consumption may depend on local availability of this resource, we incorporated *Sargassum* availability into our analysis of consumption by comparing a relative consumption index (RCI) for this taxa across habitats, where $RCI = \text{proportion of } Sargassum \text{ consumed} \times \text{proportion of } Sargassum \text{ present}$ (from algae biomass results, data averaged at site level; method modified from GPI index used by Hoey and Bellwood (Hoey & Bellwood 2009). We found equally striking differences between habitats in RCI ($F_{2,6} = 15.89$; $p = 0.004$; data not shown) as for rates of herbivory.

We found strong differences among habitats in total biomass of all roving herbivorous fish and of browsing fish alone, a pattern that was consistent at all sites (Table 2.2a, 2.2b). The reef flat and outer reef habitats generally hosted an order of magnitude higher herbivore biomass than the lagoon (Fig. 2.2a, 2.2b; PERMANOVA pair-wise tests, $p < 0.05$ for comparison between lagoon and either outer reef or reef flat). The species composition of roving herbivorous fish assemblages was different among habitats but the nature of these differences varied among sites (significant Habitat x Site interaction; Table 2.3a). Pair-wise comparisons showed that roving herbivorous fish assemblages in the three habitats were

significantly different from each other at all sites ($p \leq 0.002$ for all comparisons), but within each habitat, assemblages were only similar among sites in the reef flat and outer reef habitats, and not in the lagoon – i.e. the interaction was caused by the greater degree of variability in the lagoon. Differences in the composition of the browser fish assemblages between habitats were less consistent across sites (significant Habitat x Site interaction yielded by the PERMANOVA analysis: Table 2.3b), with significant differences among all three habitats at two of the sites (PERMANOVA pair-wise tests, $p < 0.05$ for all comparisons), but not at the other site, where only lagoon and reef flat assemblages differed (PERMANOVA pair-wise test, $p = 0.008$).

Canonical analysis of principal components (CAP) of all roving herbivorous fish yielded a high classification success of 93.1% across all habitat types (i.e. only 6.9% misclassification error). Correlations with CAP axis scores indicate that a high biomass of *Chlorurus sordidus* was characteristic of the reef flat (Fig 2.3a), where the biomass of this species was about an order of magnitude higher than that in the lagoon or outer reef. Although less abundant, *Siganus trispilos* was also characteristic of the reef flat habitat. *Scarus frenatus*, *S. prasiognathos* and *S. rubroviolaceus* characterised the outer reef habitat, with average biomass for each species in the outer reef 20 times higher than those in the other habitats. No species were identified as characteristic of the lagoon habitat; this habitat was instead characterised by a low biomass of all species. CAP of browser fish assemblages yielded a low classification success of 59.7% (Fig 2.3b). Correlations with CAP axis scores indicated that the outer reef tended to be characterised by high biomasses of *Naso unicornis* and *N. lituratus*, while the reef flat was characterised by higher biomass of *Scarus schlegeli* (Fig 2.3b).

There were differences among habitats and sites in algal cover (Fig 2.c; Table 2.2c) and among habitats in algal biomass (Fig. 2.2d; Table 2.2d). Algal cover and biomass were higher in the lagoon than in either the reef flat or the outer reef, which were similar (SNK pair-wise comparisons: Lagoon > Reef flat = Outer reef, $p < 0.05$). Differences in macroalgal species assemblages among habitats were not consistent among sites (significant Habitat x Site interaction; Table 2.3c). Lagoon and outer reef habitats differed significantly at all three sites ($p < 0.05$), but comparisons of reef flat habitat with lagoon and outer reef were not significant anywhere. CAP yielded a classification success of 70.4% across all habitat types (i.e. 29.6% misclassification error). The reef flat habitat hosted high biomass of *Lobophora variegata*, *Turbinaria ornata* and an unidentified filamentous green alga, whereas the outer reef habitat was characterised by red algae belonging to the genera *Amphiroa* and *Amansia* (Fig 2.3c). The lagoon habitat was strongly characterised by *Sargassum* species, which represented over 80% of the total algal biomass in this habitat.

Coral cover differed among habitats, but the nature of this difference varied among sites (significant Site x Habitat interaction; Fig 2.2e, Table 2.2e). Coral cover was always lower in the lagoon than in any other habitat (0 - 5% overall cover; $p \leq 0.002$ for all comparisons), but differences in coral cover between reef flat and outer reef were not consistent between sites. There were clear differences in rugosity among habitats, a pattern that was consistent at all sites (Fig 2.2f, Table 2.2f). The lagoon was the least structurally complex habitat, with rugosity values approaching 1 (mean all sites 0.95 ± 0.01 ; $p \leq 0.01$ for all comparisons), whereas the outer reef had similar rugosity values to the reef flat, which were ~50% more structurally complex than the lagoon (Fig. 2.2f).

Relationships between macroalgal herbivory and other variables

We found a near-significant logarithmic relationship between site averages for measurements of macroalgal herbivory and algal cover (Fig 2.4a; $F_{1,7} = 4.958$; $p = 0.06$; $r^2 = 0.415$) but not between macroalgal herbivory and algal biomass ($F_{1,7} = 3.26$; $r^2 = 0.318$; $p = 0.11$). In addition, there were no significant relationships between measurements of herbivory rates and total herbivorous fish biomass ($F_{1,7} = 1.392$; $r^2 = 0.166$; $p = 0.277$), or browser fish biomass ($F_{1,7} = 0.822$; $r^2 = 0.105$; $p = 0.395$). Rates of herbivory were higher in

the sites and habitats that were more structurally complex, as reflected by a strong linear relationship between rates of consumption of tethered *Sargassum* and rugosity (Fig 2.4b; $F_{1,7} = 64.82$; $r^2 = 0.90$; $p < 0.001$), where rugosity explained 90% of the variance in consumption ($r^2 = 0.90$).

Experimental test of effects of habitat and herbivory on algal consumption, productivity and chemical composition

Herbivore exclusion experiments performed with *Lobophora variegata* in high and low herbivory habitats (reef flat and lagoon, respectively) showed that changes in algae biomass were strongly influenced by the habitat in which thalli were deployed and whether thalli were caged, as shown by a Habitat x Herbivory interaction (Fig 2.5a, Table 2.4a). In the reef flat habitat, caging had an acute effect on biomass change: there was a net increase in biomass of 30% inside cages, compared to a net decrease in biomass of 30-50% in the partial and open cages (SNK pairwise comparisons: Caged > Open = Partially Caged; $p < 0.01$). In contrast, caging had no effect on algal biomass in the lagoon habitat, where there was a net increase in biomass of 30-60% in all treatments (SNK pairwise comparisons: Caged = Open = Partially Caged). The clear inference from this result is that herbivores strongly reduced *L. variegata* biomass on the reef flat, but not in the lagoon. No artefacts were associated with the structure of the cages (SNK pairwise comparisons: Partially Caged Lagoon = Open Lagoon, and Partially Caged Reef flat = Open Reef flat), i.e. the presence of cages did not confound the interpretation of the effects of herbivory on algal biomass. In the absence of herbivory, there were no differences in *Lobophora variegata* biomass accumulation between habitats (Fig 2.4a; SNK pairwise comparisons not significant: Reef flat Caged = Lagoon Caged).

Nitrogen content was significantly higher in caged algae than in open and partial cages (PERMANOVA pair-wise tests $p < 0.05$) (Fig 2.5b, Table 2.4b), but the habitat in which algae were placed had no effect on nitrogen content. In contrast, the availability of nitrogen per unit carbon (C:N ratio) was not affected by caging but was significantly influenced by the habitat in which algae were placed, with highest C:N ratios found in algae transplanted to lagoon habitats (Figure 2.5c, Table 2.4c).

Experimental test of palatability of algae from high and low herbivory habitats

We detected no significant difference in area loss between lagoon and reef flat morphotypes of *Lobophora variegata* after 5 days of deployment (Fig 2.6a; $t = -0.6359$, $df = 12$, $p = 0.537$, 95% CI = -4.006, 1.416). The two morphotypes did not differ in their nitrogen content (Fig 2.6b; Welch's $t = 0.170$, $df = 4.657$, $p = 0.873$; 95% CI = -0.134, 0.153). The C:N ratio of the reef flat morphotype tended to be lower than the lagoon morphotype, although statistical differences between the two only approached significance (Fig 6c; $t = -2.057$, $df = 8$, $p = 0.074$). The 95% confidence intervals of this near-significant result were relatively wide and non-symmetrical around zero (CI = -3.757, 0.214), suggesting that a difference in C:N ratio may exist but was not detected by our test. We found no differences among morphotypes in their phenolic content (Fig 6d; $t = -0.151$, $df = 8$, $p = 0.883$; CI = -0.643, 0.564).

Effect of proximity to reef on consumption of macroalgae

Consumption of tethered *Sargassum* varied with increasing distance from the boundary between the reef flat and lagoon, and the nature of the differences among distances varied among sites (significant Site x Distance interaction; Fig 2.7, Table 2.5). Nearly 100% of the tethered algae offered in the middle of the reef flat (-25 m) and at the reef flat/ lagoon boundary (0 m) were consumed at all sites (all SNK comparisons between sites not significant). We found variable differences in consumption among sites at distances between

5 and 50 m from the reef flat/ lagoon boundary, but at all sites there was no consumption at 75 m (SNK comparisons between sites not significant). At two sites, there was either very low or no consumption at 30 and 50 m from the reef flat/ lagoon boundary, but at the third site there was still high levels of consumption at those distances (significant SNK comparisons between site 1 and sites 2 and 3 at 30m and 50m).

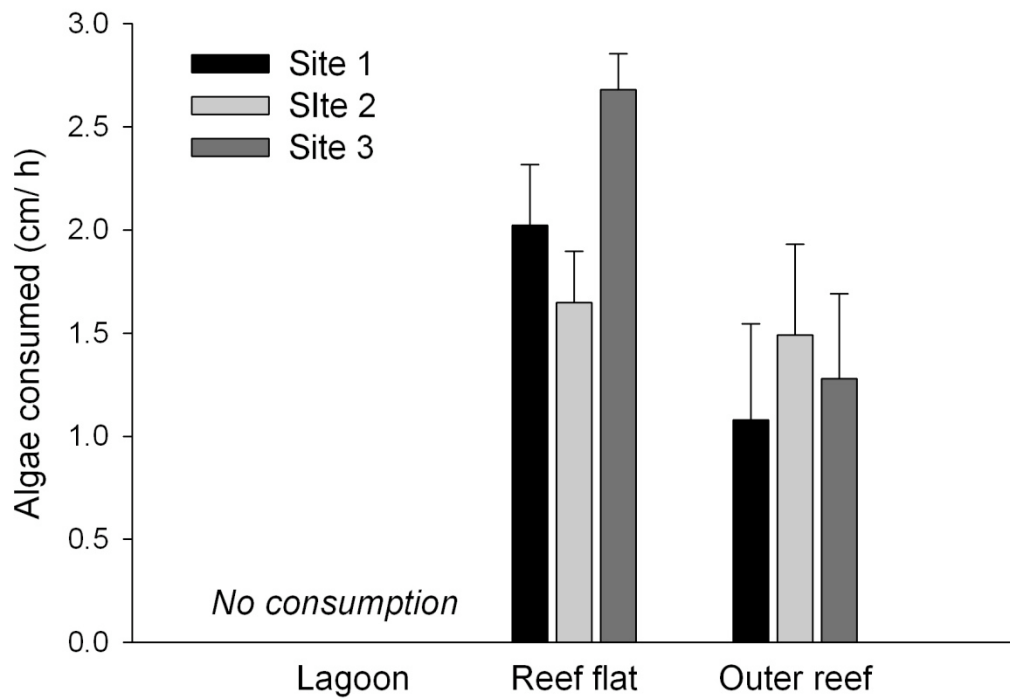


Figure 2.1. Length of *Sargassum myriocystum* lateral branches consumed per hour (mean \pm SE) at lagoon, reef flat and outer reef habitats at each of the experimental sites.

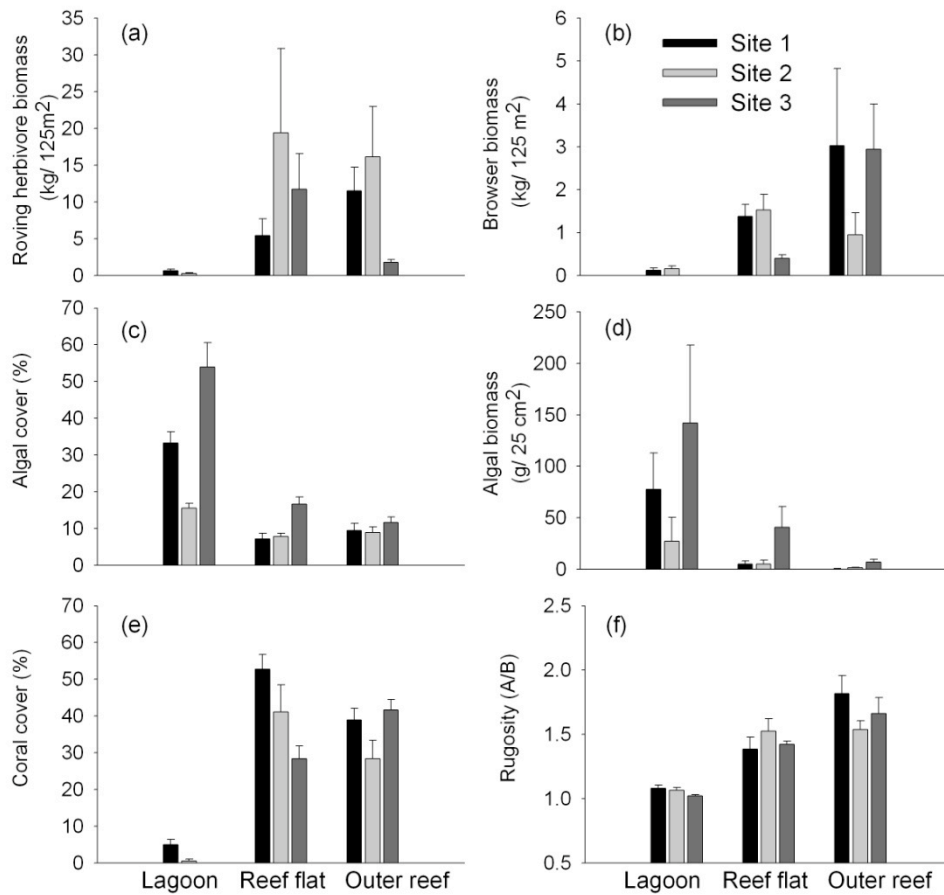


Figure 2.2. Variation between habitats in (a) total roving herbivorous fish biomass, (b) total browsing fish biomass, (c) algal cover, (d) algal biomass, (e) coral cover, and (f) rugosity. Bars represent means \pm SE.

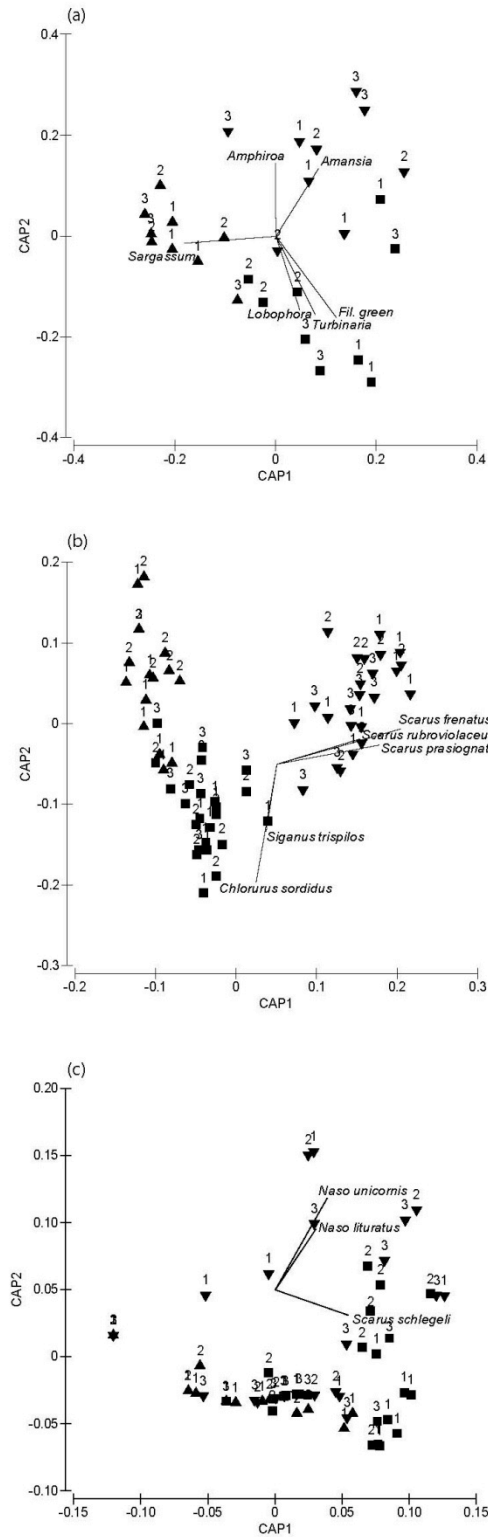


Figure 2.3. Canonical analysis of principal coordinates (CAP) comparing community assemblages of (a) all roving herbivorous fish, (b) all browsing fish, and (c) macroalgae between sites (numbered icons) and habitats (symbols): Triangles facing upwards = Lagoon; Triangles facing downwards = Outer reef; Squares = Reef flat habitat. Data were fourth-root transformed prior to ordination.

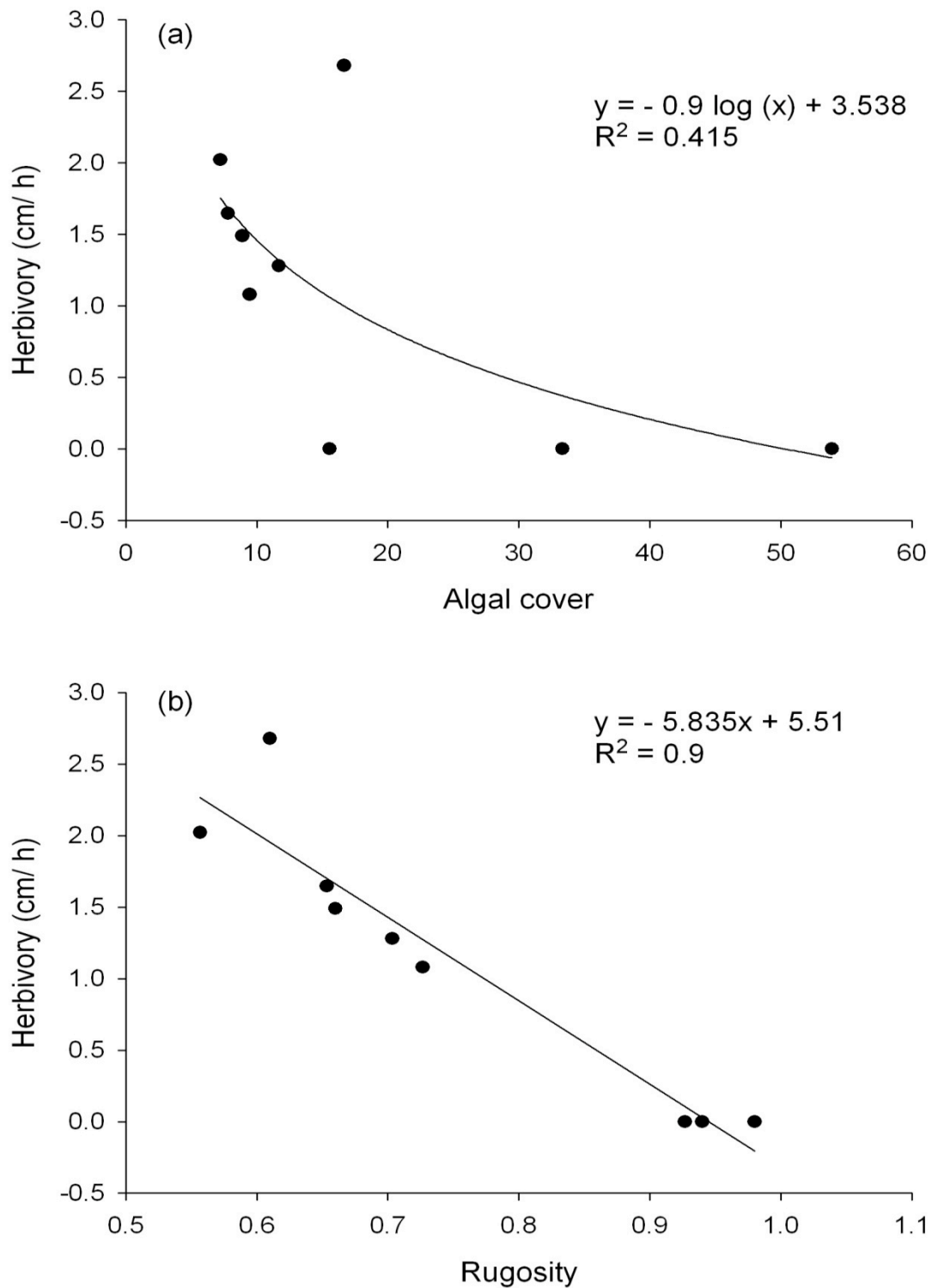


Figure 2.4. (a) Logarithmic relationship between herbivory rates and algal cover. (b) Linear relationship between herbivory rates and rugosity. All variables were averaged for each site.

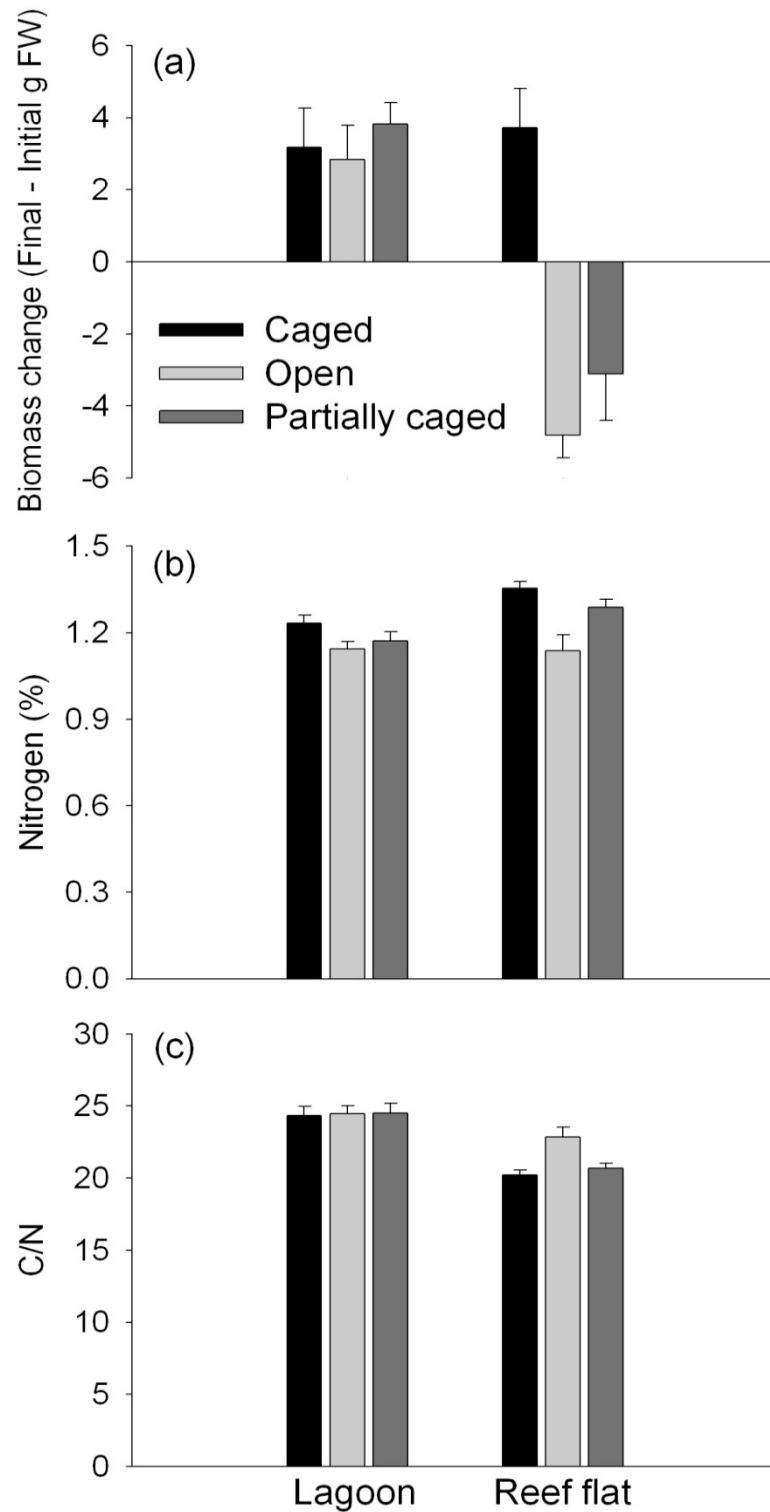


Figure 2.5. (a) Biomass change and (b) nitrogen and (c) carbon/nitrogen ratio of *Lobophora variegata* transplanted to reef flat and lagoon habitats in three experimental treatments designed to manipulate access by herbivores (Caged, Open and Partially caged) after 6 weeks. Data pooled across the three sites, bars represent means \pm SE.

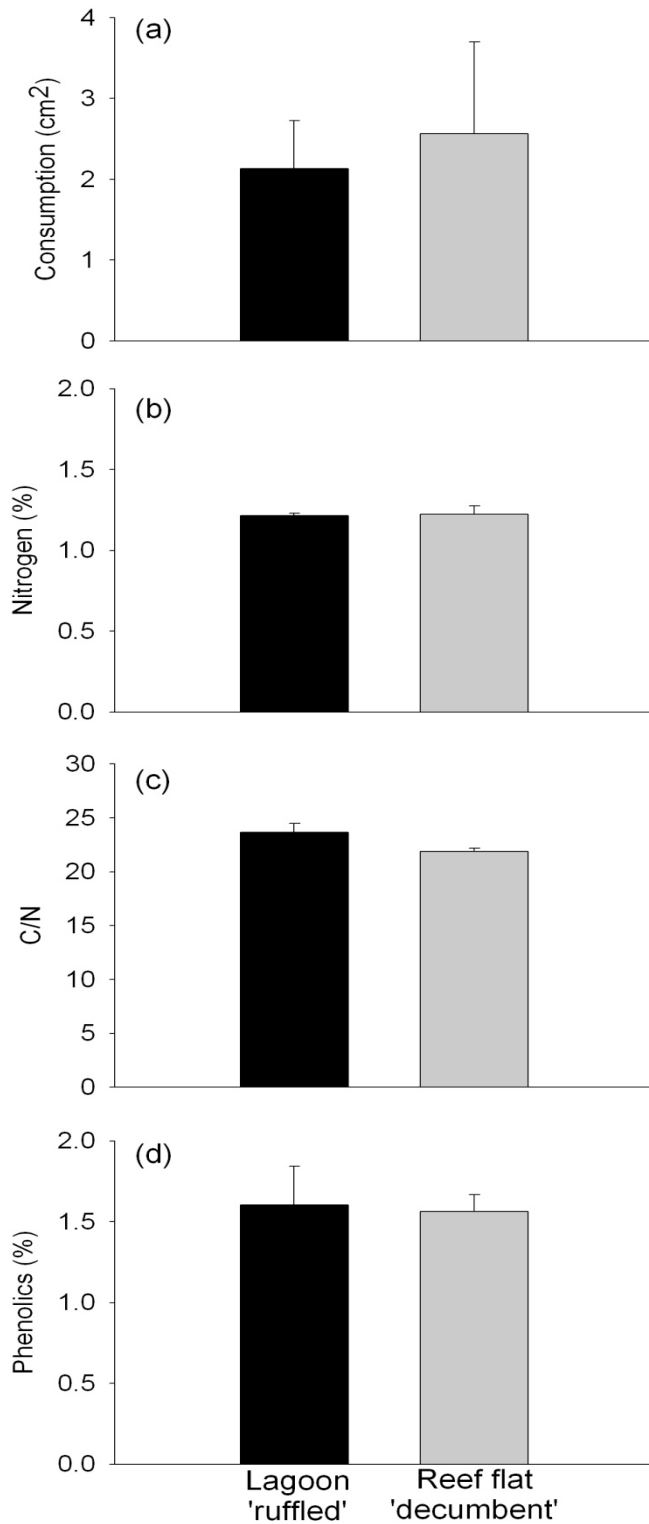


Figure 2.6. Results from reciprocal transplants of lagoon 'ruffled' and reef flat 'decumbent' morphotypes of *Lobophora variegata*: (a) rate of consumption, (b) nitrogen content, (c) carbon: nitrogen ratio, and (d) phenolic content. Bars represent means \pm SE.

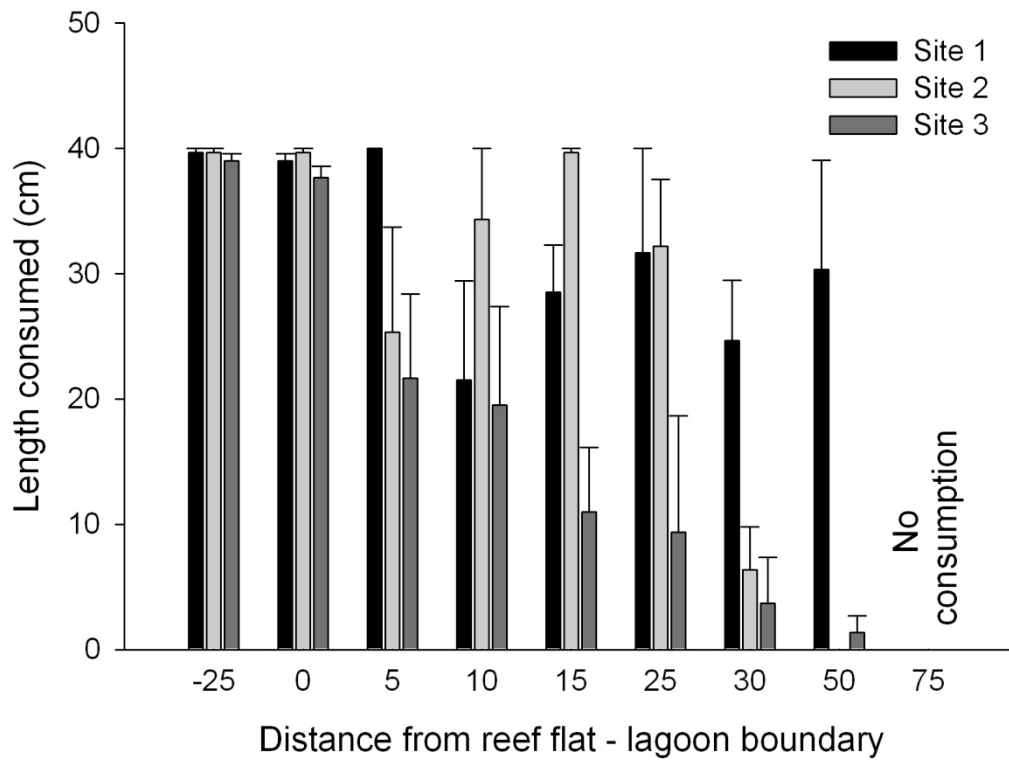


Figure 2.7. Length of *Sargassum myriocystum* lateral branches consumed after 48 hours (mean \pm SE) at increasing distances from the reef flat/lagoon boundary in the three experimental sites.

Table 2.1. PERMANOVA results on removal rates of *Sargassum myriocystum* lateral branches between sites and habitats. Relevant significant probabilities are indicated in bold.

Source of variation	df	MS	Pseudo- F	P
Site (S)	2	1.681	0.869	0.405
Habitat (H)	2	76.479	28.005	0.011
S x H	4	2.734	1.413	0.22
Residual	193	1.935		

Table 2.2. Results of the two factor PERMANOVAs assessing multivariate differences between sites and habitats in assemblages of (a) all roving herbivorous fish, (b) browser herbivorous fish and (c) algae. All data were fourth-root transformed prior to analyses. Significant probabilities are indicated in bold.

Source of variation	(a) All roving herbivores				(b) Macroalgal browsers				(c) Algae			
	df	MS	Pseudo-F	P	df	MS	Pseudo-F	P	df	MS	Pseudo-F	P
Site (S)	2	5895.1	4.6235	0.001	2	2416.2	1.5877	0.116	2	1832.8	1.6993	0.089
Habitat (H)	2	40310	6.5499	0.005	2	15085	2.9007	0.034	2	5446	2.340	0.051
S x H	4	6154.3	4.8268	0.001	4	5200.5	3.4173	0.001	4	2327.2	2.1576	0.006
Residual	63	1275			63	1521.8			18	1078.6		

Table 2.3. Results of the two factor univariate analyses assessing differences in (a) all roving herbivores and (b) macroalgal browsers and (c) algal cover and (d) total algal biomass between sites and habitats (a - b PERMANOVA; c - f ANOVA). Significant probabilities are indicated in bold. Pooling procedure was used in accordance to Underwood (1997). Tested against the pooled term = S x H + Residual. * all roving herbivorous fish analysis MS = 1.93 x 108, df = 67; † browser fish analysis MS = 4.34 x 106, df = 67; ‡ algae analysis MS = 1.99, df = 22

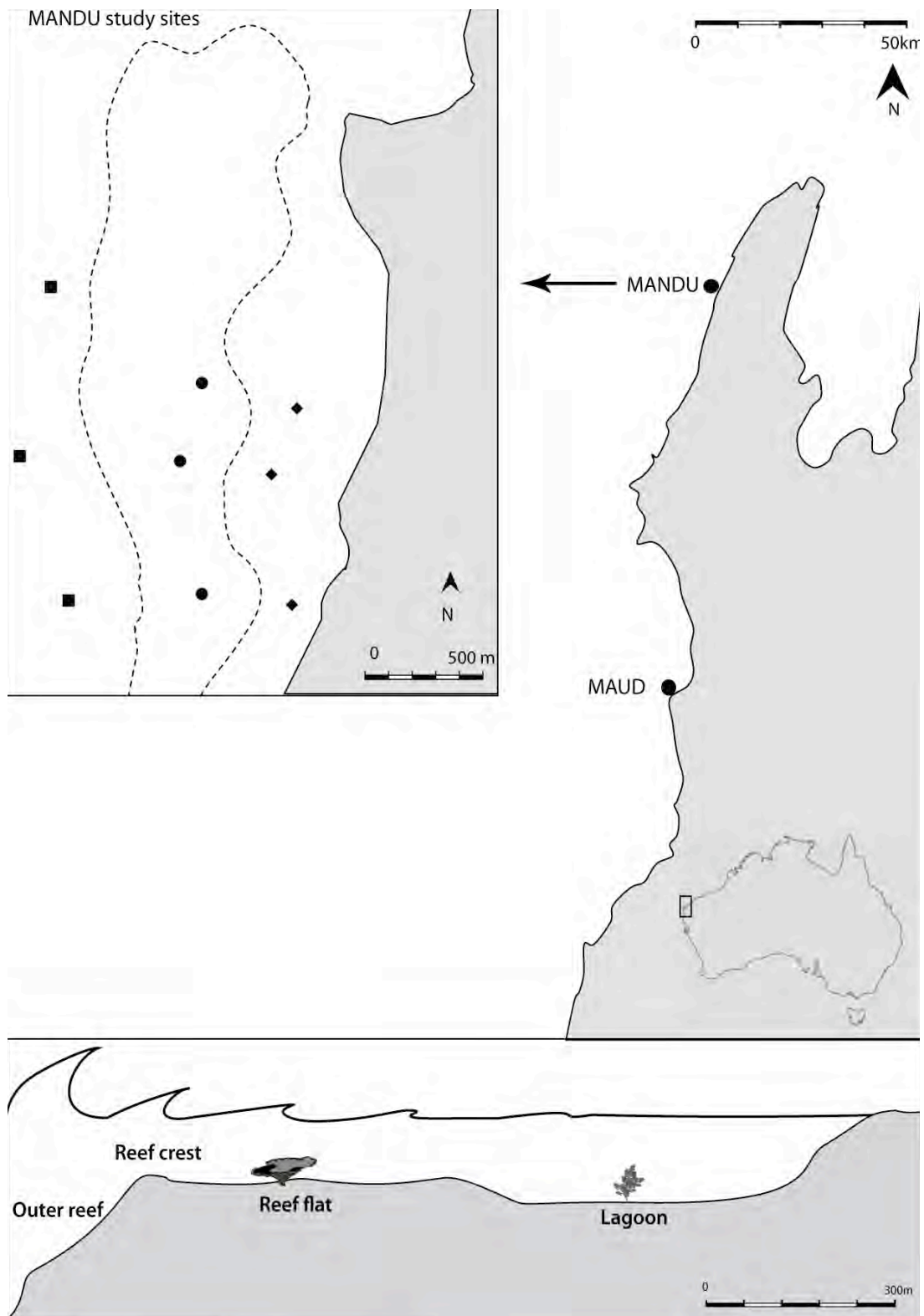
(a) All-feeding herbivores					(b) Macroalgal browsers					(c) Algae cover				
Source of variation	df	MS	Pseudo-F	P	df	MS	Pseudo-F	P	df	MS	F	P		
Site (S)	2	3.74 x10 ⁸	1.93*	0.116	2	2.42 x10 ⁶	0.551†	0.598	2	1.463	9.41	< 0.001		
Habitat (H)	2	1.03 x10 ⁹	5.30*	0.003	2	2.95 x10 ⁷	6.701†	0.004	2	4.612	13.42	0.017		
S x H	4	1.86 x10 ⁸	0.96	0.464	4	5.84 x10 ⁶	1.357	0.264	4	0.344	2.21	0.083		
Residual	63	1.94 x10 ⁸			63	4.31 x10 ⁶			45	0.1554				
(d) Algae biomass					(e) Coral cover					(f) Rugosity				
Source of variation	df	MS	F	P	df	MS	F	P	df	MS	F	P		
Site (S)	2	4.216	2.11†	0.145	2	474.07	5.512	0.008	2	0.010	0.50	0.617		
Habitat (H)	2	13.803	6.91†	0.005	2	8155.6	21.327	0.028	2	0.876	25.52	0.005		
S x H	4	1.392	0.65	0.633	4	382.41	4.446	0.005	4	0.034	1.74	0.185		
Residual	18	2.133			18	3870.4			18	0.020				

Table 2.4. ANOVA results on (a) biomass change and PERMANOVA results on changes in (b) nitrogen and (c) C/N of *Lobophora variegata* transplanted specimens in lagoon and reef flat habitats over the three sites. Pooling procedure was used in accordance to Underwood (1997). Relevant significant probabilities are indicated in bold. * Tested against the pooled term = S x H x He + Plot (SxHxHe); MS = 48.5, df = 40

Source of variation	(a) Biomass change				(b) Nitrogen				(c) Carbon/ Nitrogen			
	df	MS	F	P	df	MS	Pseudo F	P	MS	Pseudo F	P	
Site (S)*	2	21.457	0.44	0.646	2	4.273 x10 ⁻²	1.44	0.267	1600	0.143	0.873	
Habitat (H)	1	884.615	22.81	0.0412	1	0.147	6.834	0.107	300.94	96.42	0.007	
Herbivory (He)	2	280.023	7.87	0.0411	2	0.256	12.03	0.016	24.591	2.609	0.18	
Plot (SxHxHe)	36	48.040	2.89	<0.001	32	3.078 x10 ⁻²	1.827	0.019	11.619	1.815	0.017	
S x H	2	38.780	0.8*	0.457	2	2.139 x10 ⁻²	0.721	0.453	2985	0.77	0.77	
S x He	4	35.576	0.73*	0.575	4	2.117 x10 ⁻²	0.709	0.597	9450	0.834	0.505	
H x He	2	277.880	5.73*	0.007	2	5.459 x10 ⁻²	0.839	0.492	21.839	1.597	0.311	
S x H x He	4	52.648	1.1	0.377	4	6.59 x10 ⁻²	2.206	0.099	13.751	1.219	0.323	
Residual	108	16.648			92	1.684 x10 ⁻²			6400			
Residual	63	1.94 x10 ⁸			63	4.31 x10 ⁶			2.133			

Table 2.5. ANOVA results on removal of *Sargassum myriocystum* lateral branches at three sites and nine distances from the reef flat/ lagoon boundary. Relevant significant probabilities are indicated in bold.

Source of variation	df	MS	F	P
Site (S)	2	1084.114	15.63	<0.001
Distance (D)	8	1561.181	6.91	<0.001
S x D	16	225.781	3.26	<0.001
Residual	54	69.364		



APPENDIX Figure 1. Study area: Mandu and Maud sanctuary zones in Ningaloo Reef, Western Australia. In Mandu, there were three sites within each habitat: lagoon (diamond icons), reef flat (circle icons) and outer reef (square icons).

Discussion

Herbivores operate in dynamic systems where they can both generate spatial heterogeneity and respond to existing patterns in space. In this study, we found marked spatial variation in the abundance, composition and consumption of macroalgae across a coral-reef seascape. Spatial patterns in macroalgal consumption were best explained by differences in structural complexity among habitats: herbivory was always highest in the most structurally complex coral-dominated reef flat and outer reef habitats. In contrast, the cover and biomass of macroalgae appeared to be themselves influenced by consumption patterns, with habitats supporting high biomass of herbivores also supporting low algal abundance. Experimental exclusion of herbivorous fish in different habitats supported the conclusion that these consumers exert a strong influence on macroalgae in the structurally-complex reef flat habitat, but not in the structurally-simple lagoon habitat. In addition, algal consumption decreased to undetectable levels within 75 m of coral structure into the structurally simple lagoon habitat, where highly palatable macroalgae were abundant. Although productivity and nutritional quality of plants can both influence and be influenced by herbivory in terrestrial systems [12,13,14], we found no evidence that these traits affect the distribution of herbivory in the coral-reef seascape at Ningaloo Reef.

Seascape patterns in the distribution of macroalgae, herbivores and herbivory

The pattern of among-habitat differences in macroalgae cover and biomass and of biomass and composition of roving herbivorous fish in Ningaloo Reef across distances of hundreds of meters is remarkably similar to patterns observed across tens of kilometers in coral reefs with different geomorphology, such as the Great Barrier Reef (GBR). Macroalgal cover in the lagoon in Ningaloo ranged between 10-80%, values that are similar to inner shelf systems in the GBR (36-66%), while the outer reef at Ningaloo (located about 1 km offshore) hosted <10% algal cover, values that are more similar to mid-shelf or outer-shelf reefs located 50-100 km offshore in the GBR (0-15%) (Wismer et al. 2009, Hoey & Bellwood 2010a). This pattern is also apparent when comparing herbivorous fish biomass, which ranged from < 1 kg/ 125 m² in the lagoon to up to 20 kg/ 125 m² in the reef flat and outer reef, a difference that is in the same order of magnitude as the disparity in roving herbivorous fish biomass among inner-shelf and mid/outer-shelf reefs in the GBR (Wismer et al. 2009, Hoey & Bellwood 2010a).

The distinct spatial patterns in consumption of algae described in this study are also similar to the GBR (McCook 1997, Fox & Bellwood 2007), as well as to reefs found in the Caribbean (Hay 1981b, Lewis & Wainwright 1985, Valentine et al. 2008), and in the Hawaiian Islands (Stimson et al. 2001). Herbivory is always highest in coral-dominated habitats near or at the reef crest, and decreases with either depth or distance towards the inner sections of lagoons. This suggests that a similar process (or combination of processes) may be controlling the distribution of herbivory in different coral-reef ecosystems, despite great variations in their geomorphology and physical influences.

Relationship between patterns in herbivory and macroalgal distribution, productivity, nutritional quality and palatability

We found a near-significant negative logarithmic relationship between algal cover and algal consumption that suggests that the cover of macroalgae is reduced under high herbivory conditions, but it also depends on other factors under low herbivory conditions. The conclusion that this relationship is causal, rather than just correlative, is supported by the growth in macroalgae with experimental exclusion of herbivores. We did not detect a similar relationship between macroalgal biomass and herbivory, probably because much of the algal biomass collected in our quadrats was present under coral plates and in small crevices that

were effectively inaccessible to consumers, whereas algae surveyed as percentage cover better reflect algae that is available to herbivores.

Spatial patterns of macroalgal consumption were not related to among-habitat differences in macroalgal production (measured as biomass change) or nutrient content, since these algal traits were similar in habitats with contrasting levels of herbivory. Experimental exclusion of herbivores resulted in very similar growth of *Lobophora variegata* transplanted to the high herbivory reef flat and low herbivory lagoon. Similarly, we did not find any among-habitat differences in the nitrogen content of algae. We did, however, detect some differences between habitats in the availability of nitrogen per unit carbon, which tended to be higher for thalli placed in the reef flat (i.e. lower C:N ratio). Lower C:N ratios are generally associated with higher palatability, and many marine herbivores are known to preferentially consume and grow faster on diets with low C:N ratios (Barile et al. 2004, Van Alstyne et al. 2009). However, in our feeding preference experiment between reef flat-decumbent and lagoon-ruffled *L. variegata*, the two morphotypes were equally consumed, despite near-significant differences in C:N ratio. This contrasts with the findings of Coen and Tanner (Coen & Tanner 1989), who found striking differences in susceptibility to herbivory between the same morphotypes in the Caribbean and suggested that their different morphologies were related to differential grazing intensities in their respective habitats. However, these authors also found greater chemical differences among morphotypes than detected in our study, which may explain the discrepancy with our results.

Differences in the algal assemblages from habitats with contrasting levels of herbivory are consistent with the inference that macroalgal consumers are influencing spatial patterns in macroalgal community composition. The habitat with the lowest rates of herbivory (lagoon) was characterised by high abundance of palatable *Sargassum* species, which are readily eaten by macroalgal browsers worldwide when accessible (pers. obs.; (Randall 1967, McClanahan et al. 1994, Hoey & Bellwood 2009, Hoey 2010) and are actively selected by siganids (Mantyka & Bellwood 2007a). Of the algae that characterised reef flat habitats, *Turbinaria ornata* is considered unpalatable (Bittick et al. 2010), while *Lobophora variegata* is consumed by browsers to varying degrees (pers. obs.; (Randall 1967, Lewis 1985, Steinberg & Paul 1990, Diaz-Pulido et al. 2009, Bennett et al. 2010). Outer reef habitats with similar levels of herbivory were characterised by the red algae *Amphiroa* sp. and *Amansia* sp., both of which are actively avoided by some siganids (Von Westernhagen 1974, Mantyka & Bellwood 2007a). These findings are consistent with other studies that show a restriction of palatable species to areas of the reef with low levels of herbivory (Hay 1984, McCook 1997).

Feedback mechanisms between herbivory and algae

In many terrestrial systems, herbivores have a positive effect on the plants they consume through enhancing nutrient recycling and availability, a feedback mechanism known as grazing optimisation (McNaughton et al. 1997, De Mazancourt et al. 1998, Augustine et al. 2003). However, in our cage experiments macroalgae that were exposed to herbivores had the lowest nitrogen concentrations. Our results are consistent with several marine studies that show a short-term reduction in nitrogen content in seagrasses grazed by fish and urchins (Alcoverro & Mariani 2005) (Vergés et al. 2008). This lack of a fertilisation effect may be partly due to the fact that the localised input of nutrients that occurs in terrestrial systems via the faeces and urine of herbivores is likely to be reduced in the marine environment, generally due to the dilution and dispersion of nutrients via water movement. Indeed, the only marine examples where optimisation effects have been recorded through excretion of nitrogenous wastes of herbivores are from shallow, poorly flushed systems (Fong & Desmond 1997). Other examples of grazing optimization effects in the marine environment come from systems dominated by specialist herbivores such as turtles, who generally raise the nitrogen content of seagrasses through increasing the proportion of nutrient-rich new foliage by repeated cropping (Bjorndal 1980, Zieman et al. 1984, Aragones et al. 2006). Additionally, herbivores can also indirectly enhance the nitrogen content of macrophytes by

inducing bacterial nitrogen fixation either through sediment disturbance (e.g. effects of dugongs on seagrass meadows; Aragones et al. 2006) or by removing algal recruits and facilitating dominance by rapidly colonising nitrogen-fixing cyanobacteria (Munday et al. , Wilkinson & Sammarco 1983). While the lack of nitrogen enhancement of transplanted algae in our cage experiment could be partly due to the short duration of the trial (6 weeks), the fact that we found no differences in the nitrogen content of *Lobophora variegata* specimens from habitats with contrasting levels of herbivory (lagoon and reef flat morphotypes) indicates that potential differences in nitrogen fixation or other nitrogen uptake mechanisms between habitats are not having an effect on macroalgal nitrogen content in Ningaloo Reef.

Herbivory patterns explained by structural complexity

In this study, structural complexity was identified as the key feature mediating spatial patterns of macroalgal consumption by fish. This conclusion is supported by three lines of evidence: (1) different outcomes from experimental exclusion of herbivorous fish in structurally-complex reef habitat and structurally-simple lagoon habitat, (2) a strong linear relationship between macroalgal consumption and structural complexity; and (3) a decrease in herbivory with increasing distance from structurally-complex reef habitat. These results are consistent with other studies that have shown an increase in herbivore density and grazing rates with topographical complexity (Hay et al. 1983b, McCook 1997, McClanahan 1999, Valentine et al. 2008). Although there is a lack of experimental studies identifying the specific causes that link herbivory and structure, availability of shelter or refuges, increased diversity of microhabitats and resource partitioning are thought to be key influences (Vanderklift et al. 2007). Complex habitats can reduce predation by providing shelter (Hixon & Beets 1993), lower competition through increased niche availability (Jones & Syms 1998, Munday & Jones 1998), and provide specific settlement habitat for larvae (Jones et al. 2004). Nevertheless, greater structural complexity is not associated with higher herbivory at all spatial scales. For example, herbivory is lower within branching coral habitats that are highly structured at small scales (cm) than in nearby planar coral habitats (Bennett et al. 2010).

Understanding the mechanisms that drive spatial patterns of ecological processes in coral reefs is particularly important for the management of these systems, because the ability of individual coral reefs to reorganise and maintain ecosystem function following disturbance is considered to strongly depend on the matrix of adjacent reefs and habitats in the surrounding seascape (Peterson et al. 1998, Nystrom & Folke 2001). This study highlights the importance of structural complexity in establishing spatial patterns of macroalgal fish herbivory, an ecological process of key importance that can reverse phase shifts when algae overgrow corals following disturbances (Bellwood et al. 2006a). Structural complexity thus emerges as a critical feature of reefs that is essential for the healthy functioning of the ecosystem.

CHAPTER 3. Herbivore diversity on coral reefs: a transcontinental comparison

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Introduction

Herbivory is a key ecological process in coral reefs that supports intricate food webs and strongly contributes to the resilience of these systems, i.e. their ability to reorganise and maintain ecosystem function following disturbance (Bellwood et al. 2004; Mumby et al. 2006). In recent decades roving herbivorous fishes have been identified as key elements of coral reef communities, and overfishing of these consumers is considered to be a significant factor contributing to reef degradation worldwide. This is often linked to phase shifts from coral to macroalgal dominance (Hughes 1994; McClanahan et al. 2001; Graham et al. 2006). However, roving herbivorous fishes do not constitute an ecologically uniform group, but rather comprise an agglomerate of species with widely varying feeding modes and diets (Choat et al. 2002; Choat et al. 2004; Crossman et al. 2005) that have been broadly categorised into grazer and browser functional groups (Bellwood et al. 2004; Green and Bellwood 2009; Hoey and Bellwood 2010a). The grazer functional group, which includes excavating and scraping species (primarily parrotfishes and acanthurids), is largely restricted to consuming algal turfs and the associated material in the epilithic algal matrix (EAM, sensu Wilson et al. 2003), and can therefore only limit macroalgal abundance by consuming recruits (Bellwood et al. 2004, Green and Bellwood 2009). In contrast, browsers are able to remove large erect macroalgae and thus have the potential to reverse phase shifts once macroalgae are established on reefs (Bellwood et al. 2006a).

An extensive body of literature from a wide range of coral reef systems shows that macroalgal browsers are highly selective, and that most species feed on a small subset of the available algal species (Randall 1967; Wylie and Paul 1988; Paul et al. 1990; Burkepile and Hay 2008). Feeding selectivity has been linked to chemical and physical defences developed by many tropical algal species as a defence against herbivory (Wylie and Paul 1988; Paul et al. 1990; Targett and Targett 1990). In contrast, other tropical algal species that are highly susceptible to herbivory largely depend on spatial refuges to persist and are therefore only abundant in habitats characterised by low herbivore biomass or accessibility (Hay 1981b, 1984, Lewis 1986, Duffy and Hay 1990).

On the Great Barrier Reef (GBR), transplant experiments have shown that the abundance and distribution of *Sargassum* species is strongly influenced by herbivory (McCook 1997). Furthermore, herbivore-exclusion experiments have shown that this genus dominates macroalgal biomass in the absence of larger herbivorous fish, and has catastrophic community-level effects because it depresses the fecundity, recruitment and survival of corals (Hughes et al 2007). Despite *Sargassum* being considered susceptible to herbivory on the GBR, recent studies in this region have shown that removal of this macroalga is often dominated by only one or two browsing species (Bellwood et al. 2006b; Fox and Bellwood 2008; Cvitanovic and Bellwood 2009; Hoey and Bellwood 2009). This limited redundancy among macroalgal consumers highlights the potential vulnerability of coral reefs to disturbance and stresses the need to assess the functional role of individual species of herbivores (Hoey and Bellwood 2009). However, our knowledge of such species-specific patterns in macroalgal consumption is currently limited geographically, and there is a need to determine whether the patterns observed in specific reefs are applicable at a broader scale. In this study, we directly compare species-specific rates of *Sargassum* consumption in the southern GBR (east coast of Australia) with a coral reef system located at similar latitude in the west coast of Australia: the Ningaloo Reef. Video cameras were used to quantify rates of

macroalgal consumption by individual species and underwater censuses were performed to compare herbivorous fish communities in the two systems.

Materials and Methods

Study locations

This study was conducted between December 2008 and February 2009 in the Keppel Islands Group (23° 109S, 151° 009E) on the GBR (East Australia) and on Ningaloo Reef (22° 07S, 113° 52E) in Western Australia (Figure 3.1). The Keppel Islands Group includes 15 islands located about 18 km from mainland Australia in the southern inshore GBR, and are influenced by the Fitzroy river catchment. The Ningaloo Reef is a fringing arid-zone reef approximately 290 km in length that forms a discontinuous barrier adjacent to the North West Cape. In Ningaloo, expansive coral growth occurs within 100s of meters from the mainland and the reef crest is constantly flushed by high wave energy. At each study region, the study took place in habitats characterised by the highest herbivory levels, based on published evidence, and the most similar benthic structure, based on preliminary cross-habitat surveys. At the Keppel Islands, the study took place in the reef crest zone (~ 3 m depth at high tide). This zone displays the highest rates of herbivory and herbivore biomass across the fringing reef profile (Fox and Bellwood 2007) and is locally characterized by high coral cover (55.6 ± 4.0 %; mean \pm SE). Ningaloo Reef does not have accessible reef crests due to wave energy, and the study was instead performed in the reef flat back reef habitat (~2 m depth at high tide, hereafter referred to as 'reef flat'), which is also characterised by high herbivore biomass and the highest rates of herbivory across the fringing reef profile (Johansson et al. 2010; Vergés et al. Chapter 2) and supports high coral cover (40.7 ± 3.7 %; mean \pm SE).

Within each region, we selected three representative reefs (hereafter referred to as locations) that were all situated within sanctuary zones, to minimise the potential effect of extractive activities. The three Keppel Island locations were Olive Point (23° 09S 150° 55E), Middle Island (23° 10S, 150° 55E) and Halfway Island (23° 11S 150° 58E). The three Ningaloo locations were Mangrove Bay (21°58S, 113° 54E), Mandu (22°05S, 113° 52E), and Osprey (22°14S, 113° 52E). Within each location, two sites were haphazardly selected about 100 m apart.

Macroalgal assays and video analysis

To compare the fish community responsible for macroalgal removal in the different regions, locations and sites, the brown alga *Sargassum myriocystum* was used as a bioassay because it is a dominant species in both regions, is readily identifiable in the field, and pilot studies indicated that it was palatable and readily eaten by fish within a few hours.

At each site, ten *S. myriocystum* assays (ca. 230 g) were haphazardly deployed on the reef. Five individual assays were tethered to the dead coral substratum using a rubber band and gardening wire, and five of the assays were protected from herbivores in cages (50 x 50 x 50 cm; 1.44 cm² mesh size) to control for any biomass changes not due to herbivory by fish (e.g. handling losses and algal detachment due to water movement). Algae were deployed for approximately 4.5 hours between 8am and 4pm over three consecutive days. Fresh weight (to the nearest 0.1 g) was recorded before and after deployment. Algal biomass losses due to herbivory were calculated by randomly pairing individual treatment and control specimens (Roa 1992) and subtracting the change in biomass of the treatment specimen from the change in biomass of the control specimen (uncaged – caged). Average biomass

changes in control specimens were 10.15% of initial weight in the Keppels region and 18.66% of initial weight in Ningaloo (n = 90).

Video analysis

Two of the five treatment assays deployed at each site were filmed using a stationary underwater video camera (either a Sony DCR-HC1000E or a Sony HDR SR12 in an underwater housing) following the techniques of Hoey and Bellwood (2009). The three days at each site yielded approximately 81 hours of footage per region. Species-specific rates of macroalgal consumption were quantified following the methods detailed by Bellwood et al. (2006a). The total number of bites per fish species and size (total length, TL) was recorded from the video footage for each sampling period. To account for variation in bite size related to differences in body size, the midpoint of each size class was used to calculate mass-standardised estimates of bite 'impact' for each fish species (total number of bites \times body mass in kilograms) based on established length weight relationships from the literature (following Bellwood et al. 2006b). Forays, where rapid consecutive bites by an individual fish took place without a discernable pause, were conservatively classed as a single bite (Bellwood and Choat 1990).

Multivariate differences in the assemblages of fishes feeding on the *Sargassum myriocystum* bioassays were calculated using a three-way permutational analysis of variance (PERMANOVA) with the following factors: Region (2 levels), Location (3 levels, random, nested within Region), and Site (2 levels, random, nested within Location and Region). The Bray-Curtis distance was our metric in the multivariate analyses. Non-metric multidimensional scaling (nMDS) was used to produce two-dimensional ordinations of the similarities between multivariate fish samples. The similarity percentages procedure (SIMPER, Clarke 1993) was used to determine the fish taxa that contributed most strongly to dissimilarities between multivariate samples from the different regions. The contribution of each taxon was evaluated using the ratio of the mean overall dissimilarity between sets of samples and the standard deviation of this contribution ($m\bar{d}/SD[\bar{d}_i]$). Taxa were considered 'important' if this ratio was higher than 1 (i.e. the mean contribution was higher than the variation). All multivariate statistical analyses were performed using Primer-E v6 software (Clarke and Gorley 2006) with the PERMANOVA+ add-on package (version 1.0.1; (Anderson et al. 2008a)).

Relationship between bite rates and macroalgal removal

In order to identify the fish species that contributed most strongly to macroalgal removal on Ningaloo Reef and the Keppel Islands, we first selected the herbivorous fish species that were responsible for > 5 % of bites in each region (four species per region, see Results). We then used simultaneous multiple regression to describe the relationship between algae removed in the filmed bioassays (dependent variable) and the corresponding mass-standardised feeding rates for that particular filmed replicate of the four herbivorous fish species and all other species pooled together (predictor variables; n = 36 filmed replicates per region; one analysis per region). Multiple regression analyses were performed using R software (Version 2.9.0, R Development Team 2009).

Distribution of herbivorous fishes

The roving herbivorous fish community from each region, location and site was censused using standard underwater visual surveys. Fishes were counted on six replicate 10 minute timed swims per site during daylight hours by divers on SCUBA (avoiding 2 hours before and after sunrise) (Bellwood and Wainwright 2001). Fish counts were performed swimming at a constant speed and counting and estimating the size of fish within a 4 m wide transect (all

censuses performed by SB). The length of each transect was subsequently measured using tapes (116 ± 8.7 m mean \pm SE). Fishes were identified to species level and their total length was estimated in 5 cm size categories. Density estimates were converted to biomass using the allometric length-weight conversion $W = a * TL^b$, where W is weight in grams, TL is total length and parameters a and b are constants obtained from the literature (Froese and Pauly 2005). Counts were restricted to fishes over 10 cm TL from the families Acanthuridae, Siganidae, Kyphosidae and Labridae (parrotfishes). Individuals belonging to the species *Acanthurus auranticavus*, *A. grammoptilus* and *A. blochii* were grouped as *Acanthurus* spp. due to difficulties in identification.

Multivariate differences between the fish assemblages counted in the underwater censuses were calculated using a three-way PERMANOVA as described above. nMDS plots produced two-dimensional ordinations of the similarities between multivariate fish samples, and SIMPER was used to determine the fish taxa that contributed most strongly to dissimilarities. Univariate differences in total herbivorous fish biomass were calculated with the same three-way factorial design using the statistical package GMAV (coded by A. J. Underwood and M. G. Chapman, University of Sydney, Australia).

Results

Video analysis

We found strong regional differences in the diversity of fish species observed feeding on the algal bioassays, which was much higher in Ningaloo Reef (23 species) than in the Keppel Islands (8 species) (Figure 3.2). The number of bites recorded in Ningaloo Reef (15,792 bites) was also much higher than that recorded in the Keppel Islands over the same time period (1,085 bites). In the Keppel Islands, four species were responsible for over 95% of all mass standardised bite rates: *Kyphosus vaigiensis* (68.2%), *Naso unicornis* (10.9%), *Siganus doliatus* (10.5%) and *Siganus canaliculatus* (8.8%). The other Keppel Island fishes (four species) individually accounted for <5% of mass standardised bites. In Ningaloo Reef, the following four species accounted for over 85% of all mass standardised bite rates: *Scarus schlegeli* (29.5%), *Kyphosus vaigiensis* (24.3%), *Naso unicornis* (18.0%) and *Scarus ghobban* (10.3%). A further 19 species accounted for the rest of the bites, with each species being responsible for < 5% of mass standardised bites individually.

We also found strong differences in the mass standardised bite rates taken by the fish assemblages observed feeding on the macroalgal assays (Table 3.1a), which were clearly plotted on the nMDS ordination as two separate groups (Figure 3.4). We detected differences between the fish assemblages that fed in the different sites within each location, but not between locations within the two regions (significant Site (Location (Region)) effect in Table 3.1a). The SIMPER procedure identified two fish species that were characteristic of the Ningaloo assemblage of macroalgae-feeding fishes: *Scarus schlegeli* (mean similarity/standard deviation $m\bar{d}_i/SD[\bar{d}_i] = 1.55$) and *Scarus ghobban* ($m\bar{d}_i/SD[\bar{d}_i] = 1.11$). No species were identified as characteristic of the Keppels Islands region. Similar statistical results were obtained whether we analysed mass standardised bite rates (total number of bites \times body mass in kilograms per 4.5 h) or bite rate data (total number of bites per species per 4.5 h; statistical results not shown).

Relationship between bite rates and macroalgal removal

In the Keppel Islands, the mass standardised bites of *Kyphosus vaigiensis*, *Naso unicornis*, *Siganus doliatus*, *S. canaliculatus* (the four species individually responsible for > 5% bites) and all other species pooled, explained about 56% of the variation in the loss of algal

biomass from our assays ($F_{5, 30} = 7.6$, $p < 0.001$, adjusted $R^2 = 0.485$; Table 3.2). However, partial regressions indicated that only the mass standardised bite rates of *Naso unicornis* at Keppel Islands had a significant effect on algal biomass loss of the filmed assays (Table 3.2). The relationship between macroalgal biomass loss in Ningaloo Reef and the mass standardised bite rates of *Scarus schlegeli*, *K. vaigiensis*, *N. unicornis*, *S. ghobban* and all other species pooled was marginally not-significant ($F_{5, 30} = 2.18$, $p = 0.0833$, adjusted $R^2 = 0.144$).

Distribution of herbivorous fishes

We found strong differences in the herbivorous fish community composition between the two regions and between locations within each region (Table 3.1b). Regional differences were clearly displayed as two separate groups in the nMDS plot (Figure 3.5). SIMPER analyses identified *Siganus doliatus* as the only species characteristic of the Keppel Islands ($m\bar{d}_i/SD[\bar{d}_i] = 1.23$). Five species characterised Ningaloo Reef samples: *Chlorurus sordidus* ($m\bar{d}_i/SD[\bar{d}_i] = 3.64$), *Acanthurus triostegus* ($m\bar{d}_i/SD[\bar{d}_i] = 2.68$), *Scarus schlegeli* ($m\bar{d}_i/SD[\bar{d}_i] = 2.19$), initial phase parrotfish (scarid IP; $m\bar{d}_i/SD[\bar{d}_i] = 1.58$), and *S. ghobban* ($m\bar{d}_i/SD[\bar{d}_i] = 1.23$).

There were striking differences in species diversity, with 33 species being censused in Ningaloo Reef compared with only 16 in the Keppel Islands (Figure 3.6). Similarly, we detected significant regional differences in total biomass of all roving herbivorous fish, with Ningaloo Reef biomass values being over 13 times those of the Keppel Islands (Figure 3.3; Table 3.1c). In Ningaloo Reef, we found differences in total fish biomass between locations (SNK post-hoc tests), but not between sites in any of the two regions (Table 3.1c).

Table 3. 1. Results of the three factor analyses of variance assessing differences between regions, locations and sites in (a) Mass standardised bite rates from the fish community feeding on the algal bioassays (PERMANOVA), (b) Roving herbivorous fish community composition (PERMANOVA) and (c) Total roving herbivorous fish biomass (ANOVA). Significant probabilities are indicated in bold.

Source	(a) Feeding fish community				(b) Fish community composition				(c) Total herbivorous fish biomass			
	d f	MS	Pseudo -F	P	d f	MS	Pseudo -F	P	d f	MS	F	P
Region	1	3407 6	10.156	0.00 2	1	6664 3	11.855	0.00 1	1	85.95 8	13.57	0.02 1
Location (Reg)	4	3392. 7	1.5847	0.15 2	4	5625	3.8345	0.00 1	4	6.334	4.93	0.04 2
Site (Reg))	6	2149. 6	2.2401	0.01	6	1467. 1	1.3954	0.05 7	6	1.286	0.89	0.50 5
Residual	2 2	959.5 8			5 9	1051. 4			6 0	1.437 0		

Table 3. 2. Results of multiple regression analysis on the relationship between algae biomass loss in the Keppel Islands and the standardised bite rate of the four species responsible for >5% of all bites and all other species pooled together. Overall model: Adjusted $R^2 = 0.48$, $F_{5, 30} = 7.6$, $p < 0.001$. Significant probabilities are indicated in bold.

Source	Estimate	Estimate SE	t	p
<i>N. unicornis</i>	95.225	36.172	2.633	0.013
<i>K. vaigiensis</i>	23.646	15.997	1.478	0.150
<i>S. doliatus</i>	8.251	20.090	0.411	0.684
<i>S. canaliculatus</i>	-6.100	19.627	-0.311	0.758
Sum all other species	-15.785	46.709	-0.338	0.738

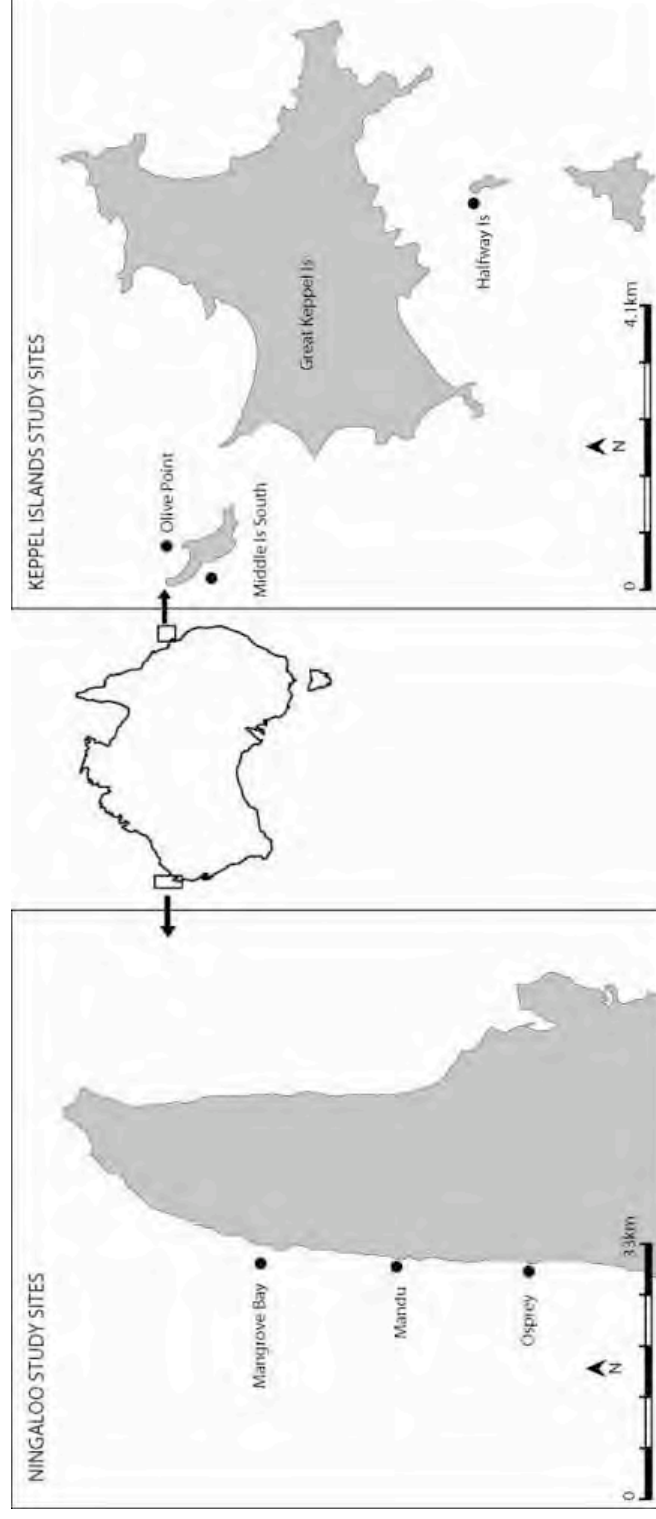


Figure 3.1. Map of the two study regions, the Keppel Islands in the southern Great Barrier Reef and Ningaloo Reef, showing the location of the study sites.

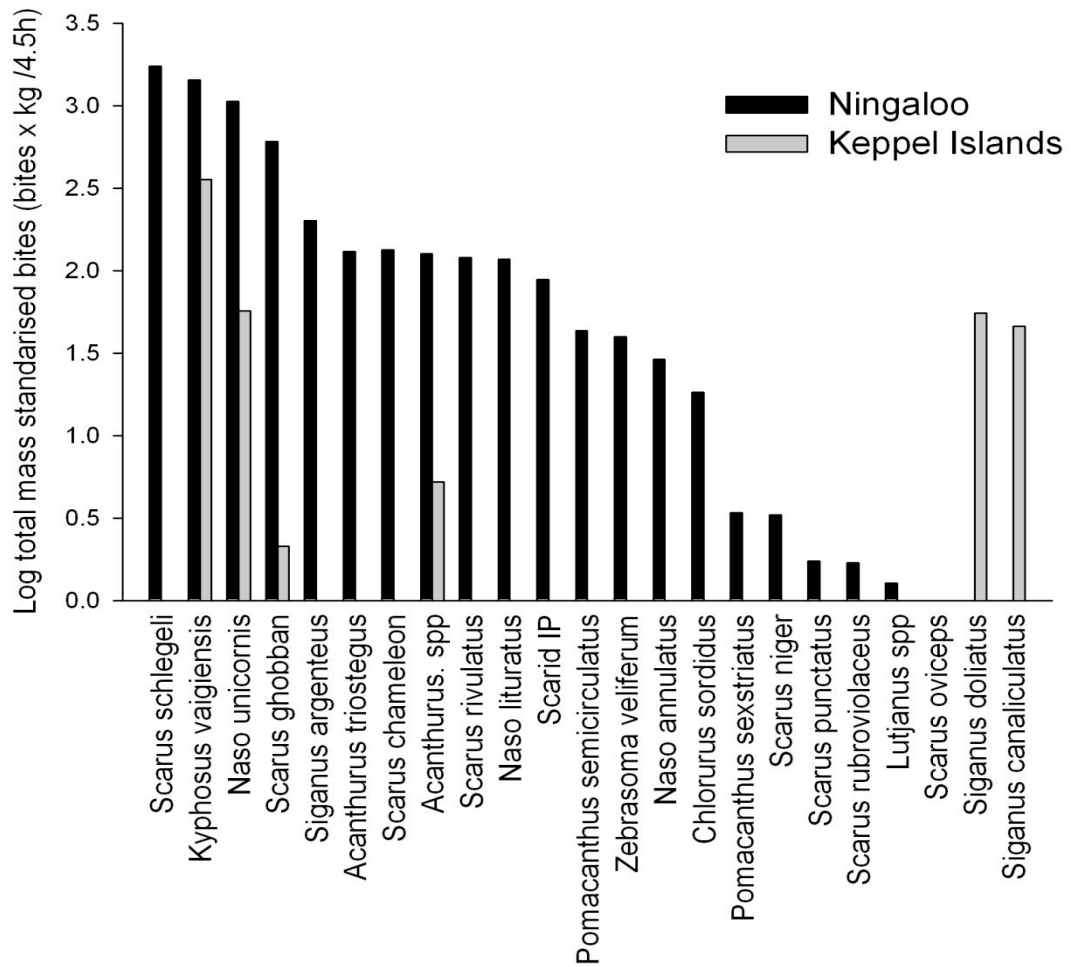


Figure 3.2. Total number of mass standardised bites (log transformed) taken by of the herbivorous fish assemblages feeding in each region over 4.5 hours ($n = 6$).

2011

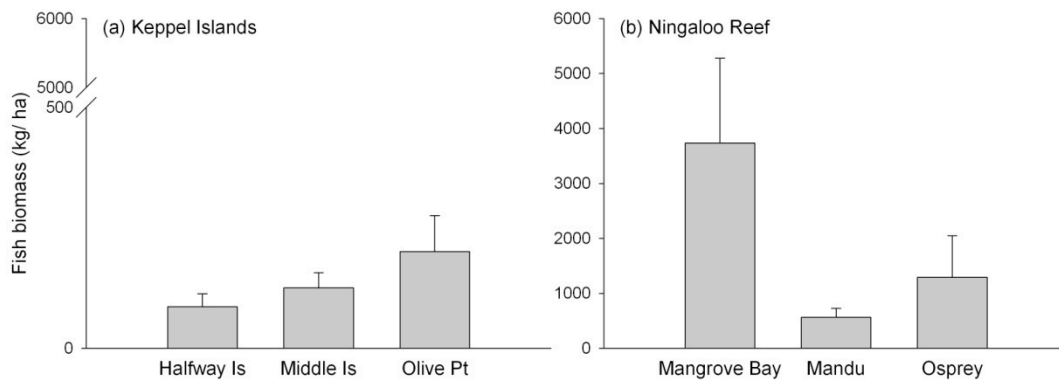


Figure 3.3. Variation between regions and locations in total roving herbivorous fish biomass ($n = 6$). Sites were not significantly different from each other and have been pooled.

2011

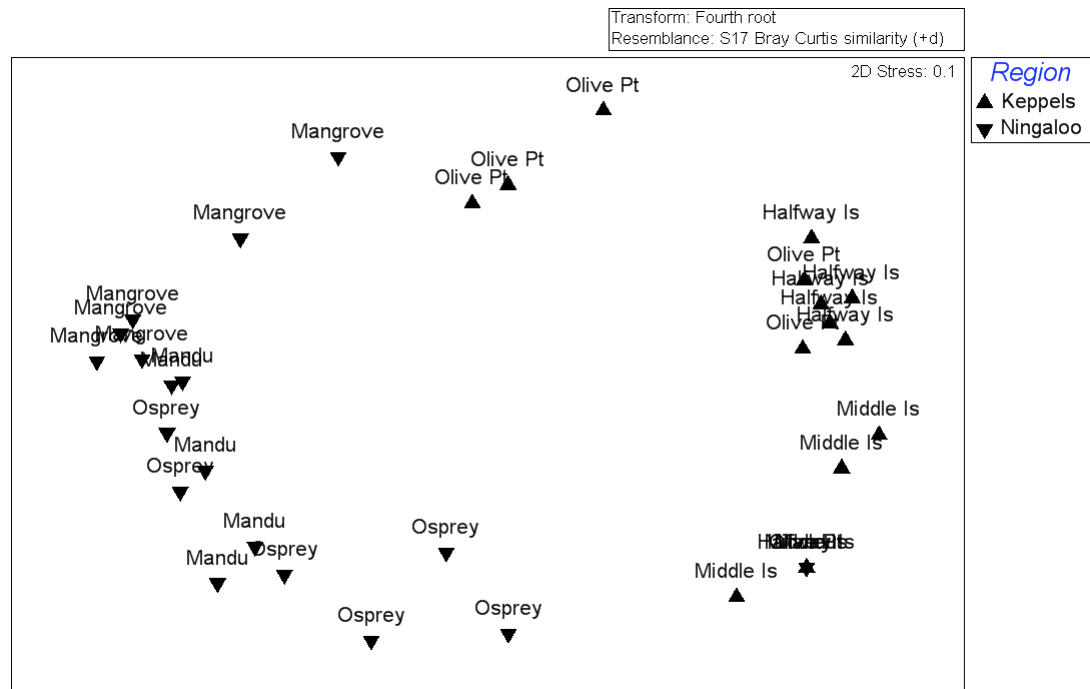


Figure 3.4. Non metric multidimensional scaling plot (nMDS) comparing the herbivorous fish assemblages feeding on the algal bioassays between regions (symbols) and locations ($n = 6$). Data were fourth-root transformed prior to ordination.

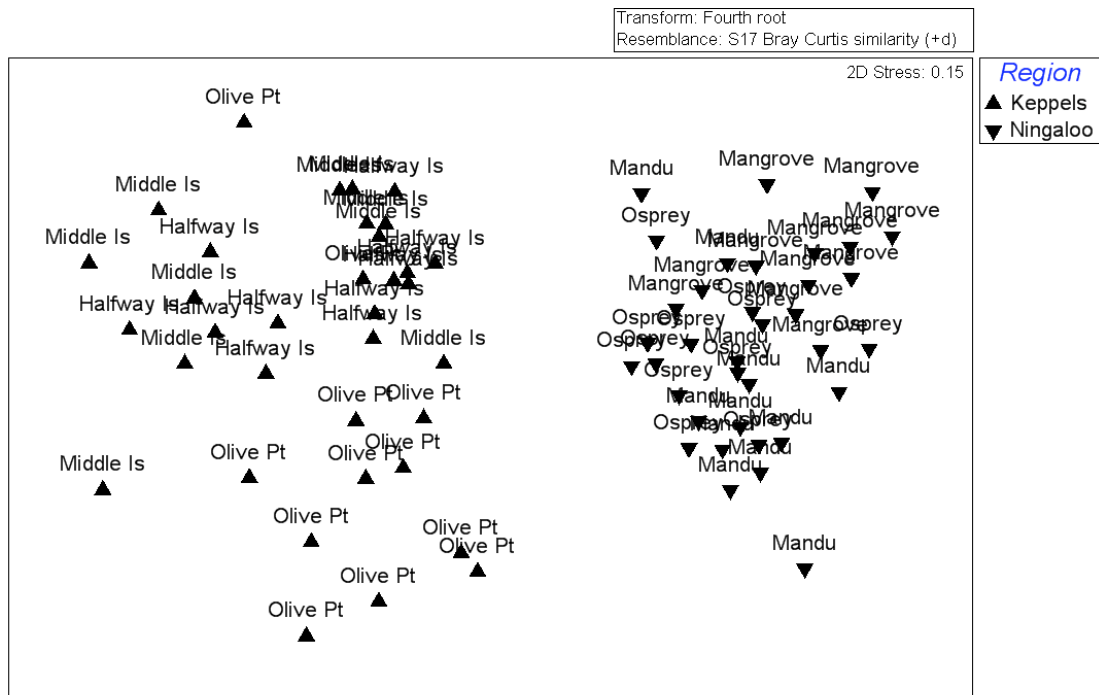


Figure 3.5. Non metric multidimensional scaling plot (nMDS) comparing the herbivorous fish assemblages between regions (symbols) and locations ($n = 6$). Data were fourth-root transformed prior to ordination.

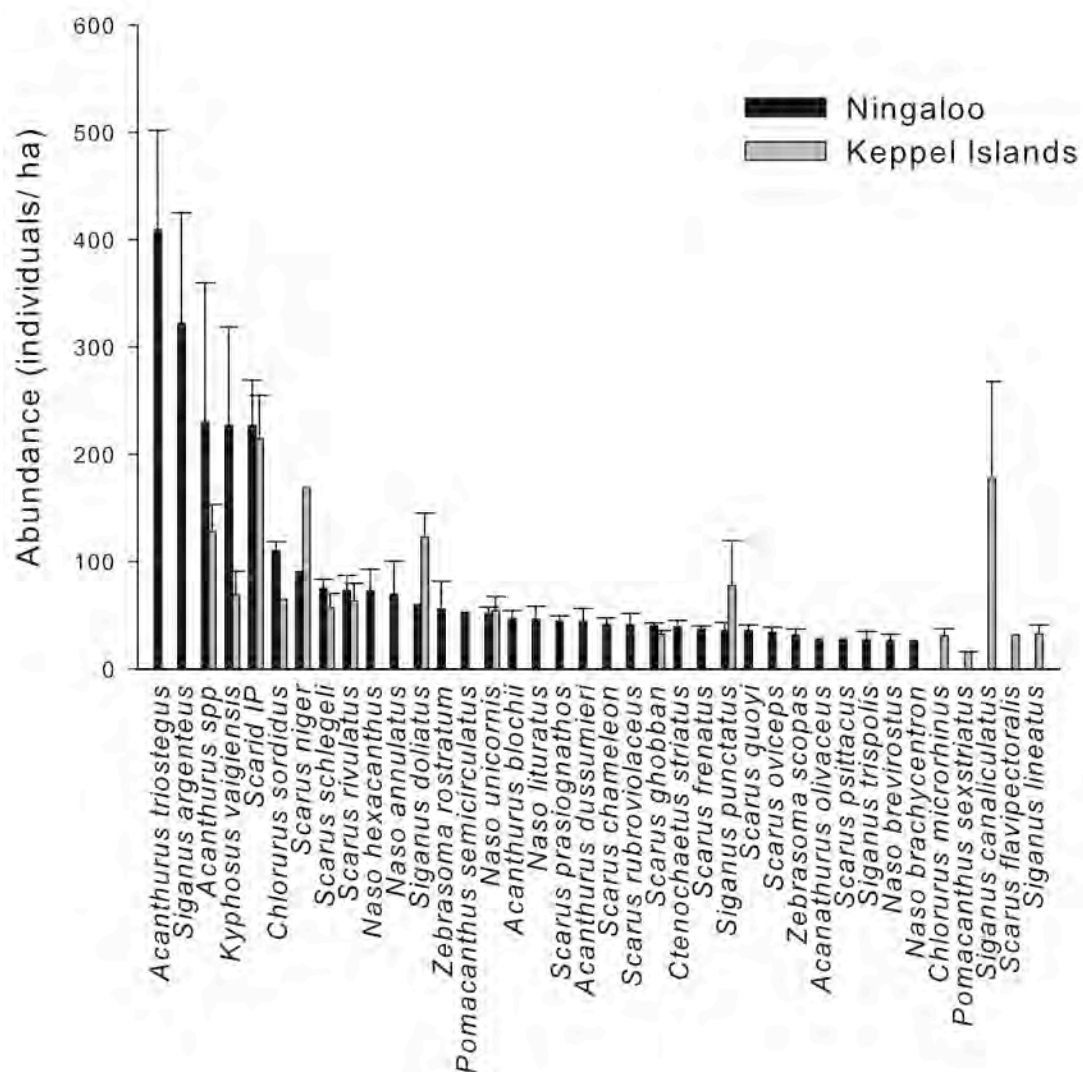


Figure 3.6. Herbivorous fish species total abundance at each region measured through underwater visual censuses ($n = 6$).

Discussion

We found strong differences between Ningaloo Reef and the Keppel Islands in both the diversity of species observed feeding on *Sargassum* and in the species composition of the roving herbivorous fish communities. The diversity of fish species recorded biting the algal bioassays in Ningaloo Reef (23 species) was much higher than in the Keppel Islands (8 species) and is one of the highest recorded in coral reefs to date (cf. 20 species in Bennett and Bellwood (2011) on the northern GBR). Video observations from the Keppel Islands confirm the role of a small number of key species previously identified as important macroalgal feeders in GBR studies, whereas consumption of macroalgae in Ningaloo Reef was spread over a larger number of less-dominant species.

In previous studies that have aimed to identify the key fish species responsible for consumption of *Sargassum* in the Great Barrier Reef, four different species have been identified as important (*Platax pinnatus*, *Kyphosus vaigiensis*, *Siganus canaliculatus*, and *Naso unicornis*), and a common pattern has emerged whereby a single species has dominated feeding at the local level (Bellwood et al. 2006b; Mantyka and Bellwood 2007b; Fox and Bellwood 2008; Cvitanovic and Bellwood 2009; Hoey and Bellwood 2009; Lefèvre and Bellwood 2010). All these previous studies were performed in the central to northern regions of the GBR. Our Keppel Islands results provide further confirmation of this pattern by highlighting the key role of one species, *N. unicornis*, in removing *Sargassum* in these southern GBR inshore reefs. Our results from Ningaloo Reef, however, provide a contrasting pattern.

In this western reef, we found a large number of fish species feeding on the algae bioassays, but none of them dominated the macroalgal removal process. *K. vaigiensis* and *N. unicornis* were two of the species responsible for the highest mass standardised bite rates in both Ningaloo (24.3% and 18.0%) and the Keppel Islands (68.2% and 10.9%, respectively) and have been recognised as important macroalgal consumers in recent studies (Cvitanovic and Bellwood 2009; Hoey and Bellwood 2009; Lefèvre and Bellwood 2010). However, the other two species responsible for the highest mass standardised bite rates in Ningaloo Reef (*Scarus schlegeli* and *Scarus ghobban*, 29.5% and 10.3% of all bites, respectively) have not been previously identified as important macroalgal feeders in any other reef system. Nevertheless, despite the very large number of bites taken by these two parrotfish species, we found no evidence that their biting had a measurable net effect on algal biomass loss in the regression analyses. It is quite likely that these two parrotfish species were not feeding on the macroalgae thallus itself, but were instead feeding on epibiota and/or on surface detritus as previously stated in *Scarus rivulatus* on the GBR (Lefèvre and Bellwood 2010). Indeed, *S. rivulatus*, like *S. schlegeli* and *S. ghobban*, have all been identified as scrapers (i.e. consumers of EAM) in studies based on their jaw morphology and field observations (Bellwood and Choat 1990).

We found striking differences in the species composition, species richness and total biomass of roving herbivorous fish between the two regions. Ningaloo Reef hosted a diverse assemblage of roving herbivores, with biomass values that were an order of magnitude higher than in the comparatively depauperate fish assemblages of the Keppel Islands. Differences in herbivorous fish communities of a similar magnitude are also observed across different continental regions of the GBR, with inshore reefs having significantly lower abundance and diversity of roving herbivores than mid-shelf and outer-shelf reefs (Williams and Hatcher 1983; Russ 1984; Wismer et al. 2009). Thus, despite Ningaloo Reef being found in close proximity to the mainland (within meters), its roving herbivorous fish community is more comparable to mid-shelf and outer-shelf reefs in the GBR than to inshore reefs such as the Keppel Islands (Johansson et al. 2010). This is probably due in great measure to a host of physical conditions that strongly limit the influence of the mainland on Ningaloo Reef. This western coast reef is constantly flushed by high wave energy and is located in an arid zone where evaporation rates far exceed annual rainfall, hence minimising terrestrial run-off and its effect on turbidity and sediment load (Cassata and Collins 2008). Additionally, anthropogenic impacts are extremely low in Ningaloo Reef, with low human populations, no agricultural activities, and very limited fishing activity. In contrast, inshore

GBR reefs are strongly influenced by increasing sediment, nutrient and pesticide loads from several degraded river catchments due to agricultural activities and other land-use practices (McCulloch et al. 2003; Devlin and Brodie 2005).

Overall, our results confirm the key role of some of the herbivorous fish species identified as important in previous studies (*Naso unicornis* and *Kyphosus vaigiensis*), but suggest that, although these species are important on the GBR, the Keppels may have limited resilience when compared to other reefs such as Ningaloo, where functional redundancy among macroalgal consumers appears to be broader. This is consistent with recent experimental evidence that shows that higher diversity of herbivorous fish can significantly lower macroalgal abundance in coral reefs (Burkepile and Hay 2008, 2010), and with a new study that integrates a long-term data set of field surveys in the GBR and further confirms a strong association between low fish herbivore diversity and a coral-macroalgal phase-shift (Cheal et al. 2010).

CHAPTER 4. Rates of *Sargassum* consumption and identity of herbivores vary across hundreds of kilometres along a continental fringing coral reef

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Introduction

Herbivory is an important ecological process that can control rates of primary productivity and the abundance of autotrophs in a wide range of terrestrial (Frank et al. 2002) and aquatic (Burkepile and Hay 2006) ecosystems. In coral-reef ecosystems, high rates of herbivory by fishes is often considered essential for the persistence of a coral-dominated state (Hughes et al. 2003, Bellwood et al. 2004), with these herbivores playing a critical role in mediating the competitive interactions between corals and benthic algae (Mumby 2009). Indeed, the removal of herbivores from an area of reef disturbance, be it through overfishing (Jackson et al. 2001), disease (Hughes 1994) or experimental exclusion (Hughes et al. 2007), often results in transitions from a coral-dominated state to one dominated by erect stands of macroalgae (Done 1992, Ledlie et al. 2007).

Herbivory by fishes within coral-reef ecosystems does not, however, represent a uniform process. Different 'nominally' herbivorous coral-reef fishes (*sensu* Choat et al. 2002) can exhibit marked variation in feeding morphology (Bellwood and Choat 1990), behaviour (Fox et al. 2009), dietary preferences (Choat 1991) and subsequent impacts on the underlying substrata (e.g. Bonaldo and Bellwood 2009). This variation can result in a suite of species playing different, but often complementary, roles in maintaining the structure and function of coral reefs (Burkepile and Hay 2008). Functionally, herbivorous fishes may be broadly classified into two distinct groups: 'grazers' and 'browsers'. Grazing fishes, including scrapers, excavators (Bellwood and Choat 1990, Bonaldo and Bellwood 2010) and other detritivores (e.g. Fox et al. 2009), which target various components of the epilithic algal matrix (EAM; *sensu* Wilson et al. 2003) and therefore influence macroalgal abundance only through the removal of algal recruits (Bellwood et al. 2004, Bonaldo and Bellwood 2010). In contrast, macroalgal browsers are responsible for the removal of substantial portions of erect macroalgae from reefs (Bellwood et al. 2006b, Hoey and Bellwood 2009). The role of this browsing functional group of herbivorous fishes therefore represents a separate and crucial ecological process, particularly in the context of reef degradation and the ability of a reef system to reverse a 'phase shift' once erect canopy-forming macroalgae have been established following a disturbance (Bellwood et al. 2006b, Hughes et al. 2007). Thus, understanding variation in the role macroalgal consumers can play within a reef system is fundamental in understanding the processes that structure coral-reef macroalgal communities, and ultimately, the health and resilience of a reef.

Traditionally, studies quantifying macroalgal herbivory by fishes have either: ignored the identity of the consumer (Lewis and Wainwright 1985, Hay 1981a); inferred a species' function based on its presence in an area (Williams and Polunin 2001); used feeding experiments in aquaria (Targett and Targett 1990); or undertaken gut-content analyses (Clements and Choat 1997). The recent use of remote video cameras, however, has provided us with a new and useful insight into the varying algal-removal roles of herbivorous fishes in coral reefs (Mantyka and Bellwood 2007a, Cvitanovic and Bellwood 2009, Lefevre and Bellwood 2011), often revealing patterns different to those based on inference alone (e.g. Bellwood et al. 2006b, Fox and Bellwood 2008, Hoey and Bellwood 2009). Within the Indo-Pacific region, much of this direct understanding of variation in rates of macroalgal removal is confined to discrete points within expansive coral reef systems. For example,

within the Great Barrier Reef (GBR), herbivory studies are largely restricted to local reefs around two islands within a system that stretches ca. 2600 km (Bellwood et al. 2006b, Mantyka and Bellwood 2007b, Fox and Bellwood 2008, Cvitanovic and Bellwood 2009; Hoey and Bellwood 2009, 2010a; but see Bennett and Bellwood 2011). While many of these spatially restricted studies share a common pattern whereby the process is dominated by a select few species within a relatively diverse fish assemblage (e.g. Hoey and Bellwood 2009), our understanding of how well these patterns can be generalised on reefs elsewhere is still in its infancy. In the present study, we therefore quantify rates of macroalgal herbivory by fishes at scales relevant to the spatial extent of Ningaloo Reef, a fringing coral-reef system abutting a continental coast. We use *Sargassum myriocystum* (hereafter referred to as *Sargassum*) tethers, the dominant alga in Ningaloo Reef in terms of biomass (Vanderklift and Vergés *unpubl. data*), and remote video cameras to quantify both local- (within-reef, <1 km) and broad-scale (regional, 50-300 km) variability in rates of herbivory and the identity of herbivores. In doing so, we also examine the relationship between *Sargassum* consumption, the composition of roving herbivorous fish assemblages and the feeding behaviour of fishes at these representative scales. Situated along the sparsely populated north-west cape of Western Australia, the Ningaloo Reef is a relatively intact arid-zone nearshore coral-reef system that provides a unique opportunity to investigate representative spatial variability in algal-herbivore interactions without the potentially confounding influences of poor water quality or overfishing.

Materials and methods

Study locations

This study was conducted during April and May 2009 on Ningaloo Reef, a fringing coral-reef that forms a discontinuous barrier approximately 290 km in length along the north-west cape of Western Australia (Figure 4.1). Within the reef, we selected five sanctuary (no-take) zones encompassing most of the latitudinal extent of the Ningaloo Marine Park (Bundegi 21°51'S, 114°10'E; Mandu 22°05'S, 113°52'E; Point Cloates 22°44'S, 113°39'E; Maud 23°05'S, 113°44'E; Gnaraloo Bay 23°45'S, 113°31'E). Within each region, three reef-flat sites were randomly selected at 2-3 m depths and spaced approximately 300 m apart (Figure 4.1). All sites were located in coral-dominated reef-flat habitat, since this habitat displays amongst the highest levels of herbivory and herbivorous fish density within the Ningaloo Reef (Johansson et al. 2010, Chapter 2).

Macroalgal tethers

Sargassum myriocystum was used to quantify variability in macroalgal removal by fishes since it represents a conspicuous, palatable (Vergés *unpubl. data*) and readily identifiable macroalga present in the adjacent lagoon habitats of most study regions. Importantly, *Sargassum* is often the dominant taxa following experimental exclusion of herbivores in many Indo-Pacific reefs such as the GBR (Hughes et al. 2007) and Ningaloo Reef (Webster 2007). *Sargassum* thalli were collected from lagoon habitats adjacent to the reef-flat in each region, with the exception of Gnaraloo Bay where there were no large algal beds and algal material was instead collected from the closest region (Maud) where *Sargassum* occurred. Care was taken to minimise damage during algal collection by maintaining holdfasts intact. Thalli were transported back to the laboratory in catch bags and intermittently submerged in seawater in order to retain their moisture and turgidity. Prior to processing in the laboratory, the basal portions of the plants were bundled with a rubber band and excess water was removed using 10 standard spins (approximately 30 s duration) on a pull-cord salad spinner. The fresh weight of the tethers was then recorded using digital scales before being assigned a random identification label. Initial weight of tethers ranged from 300 to 360 g, with a mean mass of $332 \text{ g} \pm 2 \text{ g}$ (\pm standard error) over the study period ($n = 360$ algal assays).

Processed material was maintained in catch bags in the ocean overnight until used for tethering experiments, with all plants being used within 18 h of initial collection.

Within each reef-flat site, six *Sargassum* replicates were haphazardly tethered at least 5 m apart to bare substratum using plastic-coated garden wire. Tethering wire and identification labels were concealed as much as possible to avoid any potential feeding deterrence effects to herbivorous fishes. No *Sargassum* tethers were placed within or near damselfish (Pomacentridae) territories, since territorial damselfishes can reduce the feeding rates and foraging effectiveness of other herbivorous fishes (Foster 1985). A further six control replicates were deployed and protected from all herbivores by individual exclusion cages (50 cm L × 50 cm W × 75 cm H). A mesh size of 1.5 cm² was used to minimise caging artefacts such as a reduction in water flow, while still restricting access by fishes. Each caged control tether was deployed near a treatment tether, forming a total of six paired treatment-control replicates for each sampling period. These six paired treatment-control *Sargassum* tethers were used to determine changes of biomass experienced by the algae over the deployment period due to factors other than herbivory (e.g. handling loss and abrasion). The physical proximity of the treatment-control pairs ensured that the variance in mass loss attributed to external factors jointly affected both the control and the treatment algae within a replicate pair (Prince et al. 2004). Deployment always occurred between 1000 and 1600 h during mid-tide events, as this is the daily period when fish-grazing activity is likely to be at its highest (Zemke-White et al. 2002, Fox et al. 2009). After 3.5 h, all algal tethers were retrieved and reweighed in the laboratory. This tethering procedure was repeated on two different days at each of the three reef-flat sites across all five regions of Ningaloo Reef (n = 36 treatment and n = 36 control tethered units per region). The change in fresh weight of each treatment algal specimen over the deployment time minus the change in fresh weight of its corresponding paired control provided us with a conservative measure of herbivory by fishes (i.e. uncaged – caged).

Video analysis: species-specific bite rates

Stationary, high-definition video cameras were used to determine the contribution of individual herbivorous fish species to the removal of the transplanted *Sargassum* tethers, a technique which allows accurate observations of feeding fishes without the potentially confounding effects of diver presence (Bellwood et al. 2006b, Mantyka and Bellwood 2007b). For each deployment, two video cameras (*Sony-HDR SR12* in underwater housings) were simultaneously deployed at a site, filming the feeding activity on two randomly selected uncaged tethers. Video cameras were attached to concrete blocks and placed on the seabed 2-3 m from the selected tether, ensuring the entire macroalgal unit could be viewed in the frame. During the initial seconds of filming, the camera focal length was calibrated using a scale bar of known length, which was later transposed onto the viewing monitor where it was used as a reference scale for analysing the footage. The cameras were set to film continuously for the entire 3.5 h of assay deployment. This filming procedure yielded 14 h of footage per site (i.e. 2 × 3.5 h per sample day) and a total of 42 h of footage per region.

To quantify the bite rates of herbivorous fishes, we viewed the entire 210 h of footage and counted the total number of bites taken by individual fish on each filmed tether. All feeding fish were identified to species level, with the exception of some initial phase scarids (Scaridae) and some kyphosids (Kyphosidae). Unidentifiable, dark-coloured juvenile *Scarus* species were classified together as *Scarus* I.P. (initial phase). Likewise, a larger species of kyphosid (which clearly was not *K. vaigiensis*, a dominant herbivore at Ningaloo Reef, Chapter 3) was conservatively classed as *Kyphosus* sp. (possibly *K. sydneyanus* and/or *K. bigibbus*), as it was difficult to consistently differentiate between the two species using imagery alone. A 'bite' was recorded only if the fish could be seen to apply its jaws to the tethered alga and close its mouth (following Mantyka and Bellwood 2007b). In those instances where individual bites could not be counted due to a succession of rapid bites without a discernable pause, the 'foray' was conservatively classed as a single bite event (Bellwood and Choat 1990). Bites from individuals > 10 cm total length (TL) were tallied into 5 cm size class categories. The total number of bites per fish species was then converted

into a 'mass-standardised' bite (bite count \times feeding individual's body mass in kilograms; following Mantyka and Bellwood 2007b), based on published length-weight relationships (Kulbicki et al. 2005), and using the midpoint of each size class as the feeding individual's TL. Mass-standardised bite counts were then converted to a bite rate (mass bites.min⁻¹) by dividing the count for each species by the period when the algal tether was accessible for feeding. In those instances where the tether was grazed completely to its basal portions prior to the 3.5 h period, the available potential feeding time was adjusted accordingly, since the algae was no longer present for potential feeding by other fishes for the remainder of the sampling duration. During video analysis, foraging associations were noted, with all bites from individual fishes being categorised into either group feeding (we define groups whenever individuals of one or more species forage simultaneously in association with one another; see Lukoschek and McCormick 2000) or solitary feeding categories.

Distribution of roving herbivorous fishes

The abundances of species within the roving herbivorous fish community (Acanthuridae, Scaridae, Kyphosidae and Siganidae) from each site were quantified using a series of timed visual censuses. Underwater visual censuses (UVC) were carried out on snorkel using 10-minute timed swims parallel to the contour of the reef-flat, encompassing the area of reef used for tethering experiments. The distance covered for each 10-minute transect was measured by trailing an underwater measuring tape which was fixed to the reef at the starting point of each transect (mean distance of 100.7 m \pm 0.5 m). All potentially herbivorous fish species within a 5 m wide belt-transect, extending from the reef substratum to the sea surface, were recorded on an underwater slate according to species and nearest 5 cm size class. With the exception of the readily identifiable *Chlorurus sordidus* (Scaridae), all other dark coloured initial-phase (I.P.) parrotfishes were recorded as a single group (*Scarus* I. P.). Similarly, mixed schools of fish that were likely to be a combination of *Acanthurus blochii* and *A. grammoptilus* (Acanthuridae) were classified together as *Acanthurus* spp. due to difficulties in identification. Two UVCs were carried out on each of the two days that tethers were deployed within each site ($n = 12$ per region), with a single UVC conducted immediately prior to the deployment of the tethering experiments, and another after the deployment period had ceased to minimise disturbance and any potential feeding deterrence to the herbivorous fish communities. Transect replicates within a site were separated by a minimum of 20 m each time in order to maximise independence between census events. Fish counts made from each of the UVCs were converted into abundance per unit area (individuals 100 m²) using each individual transect area. Abundance estimates were then further converted into biomass estimates (grams 100 m²) using established length-weight relationships for each species (Kulbicki et al. 2005).

Statistical analyses

Variation in rates of consumption of *Sargassum* tethers was analysed with a three-factor ANOVA testing for differences among regions (fixed factor with 5 levels), sites (random factor with 3 levels nested within each region), and days (random factor with 2 levels nested within each site and region). Analyses were based on the corrected algal mass removed by fishes from the six tethered *Sargassum* replicates deployed each sampling day. Residual plots and Cochran's test indicated that the data met the requirements of normality and homogeneity of variance. Student-Newman-Keuls (SNK) test was used to determine where the differences lie among regional means.

To examine variation in the overall feeding activity across regions, we pooled the total number of bites taken by all species for each region and tested for differences using the same three-factorial ANOVA design previously described. Analyses were based on square-root transformed bite count data to satisfy the assumptions of ANOVA. For species-specific mass-standardised bite rates ('bite rates' herein) on the filmed *Sargassum* tethers, differences among regions and sites and between days were examined using a permutational multivariate analysis of variance (PERMANOVA, Anderson 2001). The same

three-factor hierarchical design as described previously was also used for PERMANOVA. Analyses were conducted using Bray-Curtis dissimilarities to emphasise absolute differences, and were based on square-root transformed data (to reduce the effects of numerically large values from abundant schooling species; Clarke 1993) with 4999 unrestricted, random permutations. When the fixed region factor was significant, we further investigated the term through *a posteriori* pair-wise comparisons using 4999 random permutations of raw data to obtain Monte Carlo *p*-values (Anderson 2001). A canonical analysis of principal coordinates (CAP, Anderson and Robinson 2003, Anderson and Willis 2003) was used as a constrained ordination procedure to visualise and explore patterns in species-specific bite rates of all species based on the *a priori* hypothesis of differences among regions. The bite rates of species likely to be responsible for any observed differentiation among regions were determined by examining Pearson correlations (correlation coefficient of $r > 0.40$) of species-specific bite rates with the canonical axes of the CAP.

In order to identify the fish species that contributed most strongly to the removal of *Sargassum* biomass, we used a simultaneous multiple regression analysis. Bite rates of the species responsible for >5% of bites in any region (seven species, see *Results*) were simultaneously regressed against the biomass removed from the corresponding filmed *Sargassum* transplant by fishes. Species which were accountable for <5% of bites in each region were pooled into higher taxonomic groupings for the analysis. For the analysis, feeding rate data were square-root transformed to improve normality of the data. Examination of partial correlations enabled us to identify the individual species (three species, see *Results*) that had a significant effect on algal biomass loss. We then tested for differences in bite rates of these three species across regions, sites and days using permutational univariate ANOVAs that were based on Euclidean distances and square-root transformed bite rate data. To examine the influence of group feeding behaviour by these three browsers on *Sargassum* removal efficiency, we used a multiple regression analysis based on the proportion (%) of bites taken by each of the browsers as a group within each filmed replicate ($n=60$). To account for the use of proportional data, percentage group feeding data were arcsine transformed for the analysis.

The biomass of macroalgal browsers, and all roving herbivorous fishes collectively, recorded during UVCs were compared among regions, sites and days using the same three-factor hierarchical ANOVA design as described previously. Biomass data were square-root transformed to meet the requirements of normality and homoscedasticity. Significant differences in regional means were further explored using the SNK test. Relationships between the observed herbivorous fish biomass, both collectively and including macroalgal browsers only, and the reduction in transplanted *Sargassum* mass, were examined using a series of Pearson correlation analyses. For the analyses, fish biomass and herbivory data were averaged at the day within site level, with the biomass of fishes being treated as a predictor for the corresponding level of herbivory for that same period.

Results

Removal of transplanted macroalgae

Rates of consumption of tethered *Sargassum* differed among regions of Ningaloo Reef (Table 4.1), with significantly higher algal mass removed from tethers in Point Cloates (245.6 ± 15.2 g) and Gnarlaloo Bay (213.2 ± 16.2 g) than in any other region (ranging from 67.1 ± 9.2 g to 137.8 ± 19.7 g) (Figure 4.2a). Rates of consumption of tethered *Sargassum* also varied between days, but variation among sites was not statistically significant (Table 4.1).

Species-specific bite rates

Analysis of video footage yielded 32,395 bites (8,969 mass-standardised bites) from 23 fish species on the 60 filmed *Sargassum* tethers across the five regions of Ningaloo Reef (Figure 4.2). Although there was no significant variation among regions in the total number of bites by all fishes pooled (Table 4.2), the distribution of bites among taxa differed considerably across regions (Figure 4.3b). Seven species, namely *Naso unicornis*, *Kyphosus* sp., *K. vaigiensis*, *Scarus* l.P., *S. schlegeli*, *S. ghobban* and *Siganus doliatus* accounted for 95% of the bites (98% of mass-standardised bites). The bite rates of these seven species explained approximately 73% of the variation in the loss of biomass from the filmed *Sargassum* tethers (Table 4.3). However, partial regressions indicated that, after accounting for autocorrelation in the data, bite rates of only *N. unicornis*, *Kyphosus* sp. and *K. vaigiensis* were significantly correlated with the reduction of *Sargassum* biomass from the filmed tethers (Table 4.3).

The identity of species responsible for the bites observed demonstrated significant variation among regions, but not among sites within region (Table 4.4a). The *a posteriori* comparisons showed that species identity differed for each pair-wise combination of regions (Monte Carlo $p < 0.05$), with the exception of Bundegi and Gnarlloo Bay, which did not statistically differ (Monte Carlo $p = 0.1770$). Differences in bite rates and feeding assemblages among regions were highlighted by CAP, which showed a distinct separation of the five regions according to the identity of the species responsible for the bites (Figure 4.4). Pearson correlations of species-specific bite rates with the canonical axes of the CAP indicated that 10 species were correlated (correlation coefficient $r > 0.40$) with the patterns observed among regions (Figure 4.4). Bite rates of each of the three dominant browsers differed significantly among regions (Table 4.4b). Point Cloates was characterised by the feeding of *Naso unicornis*, where it exhibited significantly higher bite rates (0.83 ± 0.19 kg bites.min⁻¹) than in any other region (Figure 4.3b). The distinction of Gnarlloo Bay and Bundegi from the other regions (Figure 4.4) was largely a result of the significantly higher bite rates of *K. vaigiensis* in these regions (0.90 ± 0.19 and 0.67 ± 0.21 kg bites.min⁻¹ respectively; Figure 4.3b). Likewise, the higher bite rates of *Kyphosus* sp. was characteristic of Maud (0.72 ± 0.46 kg bites.min⁻¹), whereas Mandu was primarily characterised by higher rates of feeding by *Scarus* species (Figures 4.3b & 4.4).

Feeding behaviour

The influential browsers, *N. unicornis*, *Kyphosus* sp. and *K. vaigiensis*, were observed feeding upon the transplanted *Sargassum* as a part of a monospecific school, a multi-species group, or as solitary individuals. Group browsing associations (mixed, or monospecific simultaneous feeding) occurred in all regions, except in Mandu where group feeding by the dominant browsers was never recorded (Figure 4.3d). On average, the greatest proportions of group feeding by browsers were evident in Gnarlloo Bay (78.5 ± 8.2 % of bites) and Point Cloates (63.6 ± 6.6 % of bites), broadly reflecting regional patterns in *Sargassum* removal (cf. Figures 4.3a & d). This variation in feeding behavior by the macroalgal browsers led to significant positive relationships between the group feeding activities of these species (collectively and individually) and *Sargassum* removal efficiency (Table 4.5).

Relationship between herbivore distribution and macroalgal removal

The collective biomass of roving herbivorous fishes varied significantly across regions (Table 4.6), however, the composition of fishes was dominated by species other than the dominant macroalgal browsers (Figure 4.3c). Collectively, *N. unicornis*, *Kyphosus* sp. and *K. vaigiensis* accounted for only 1-7% of herbivorous fish biomass across regions, yet were responsible for 85-99% of the bite rates on *Sargassum* being quantified in these regions (except in Mandu, where browsers were depauperate) (cf. Figures 4.3b & c). Rates of herbivory could not be predicted based on the distribution of macroalgal browsers in each area, as no

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relationship was evident between the consumption of *Sargassum* and the biomass of macroalgal browsers collectively, or individually (Table 4.7).

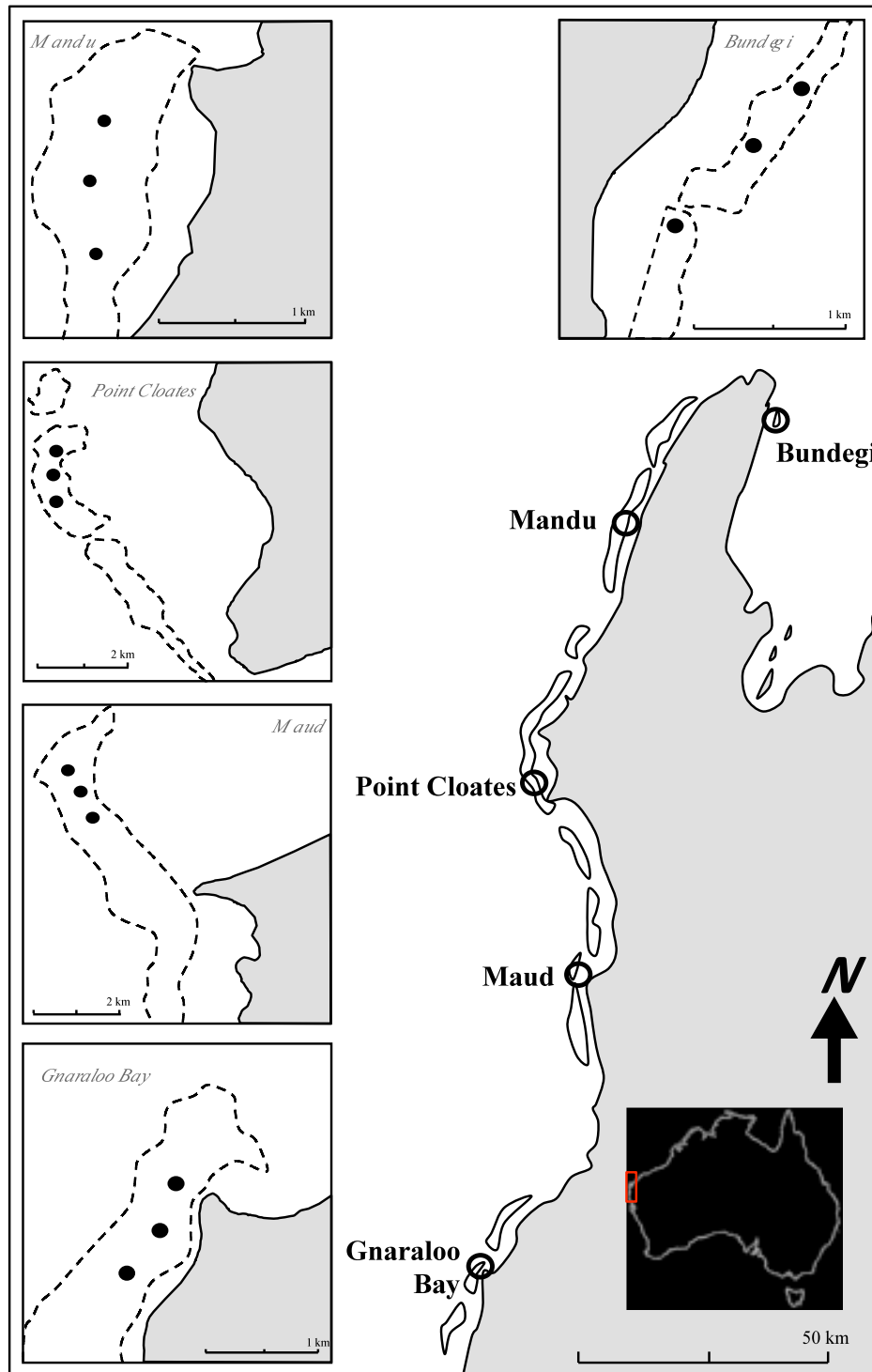


Figure 4.1. Map of the Ningaloo Reef, Western Australia, indicating the regions (open circles) and sites (filled circles in insets) studied. Dashed polygons depict predominantly coral reef-flat areas.

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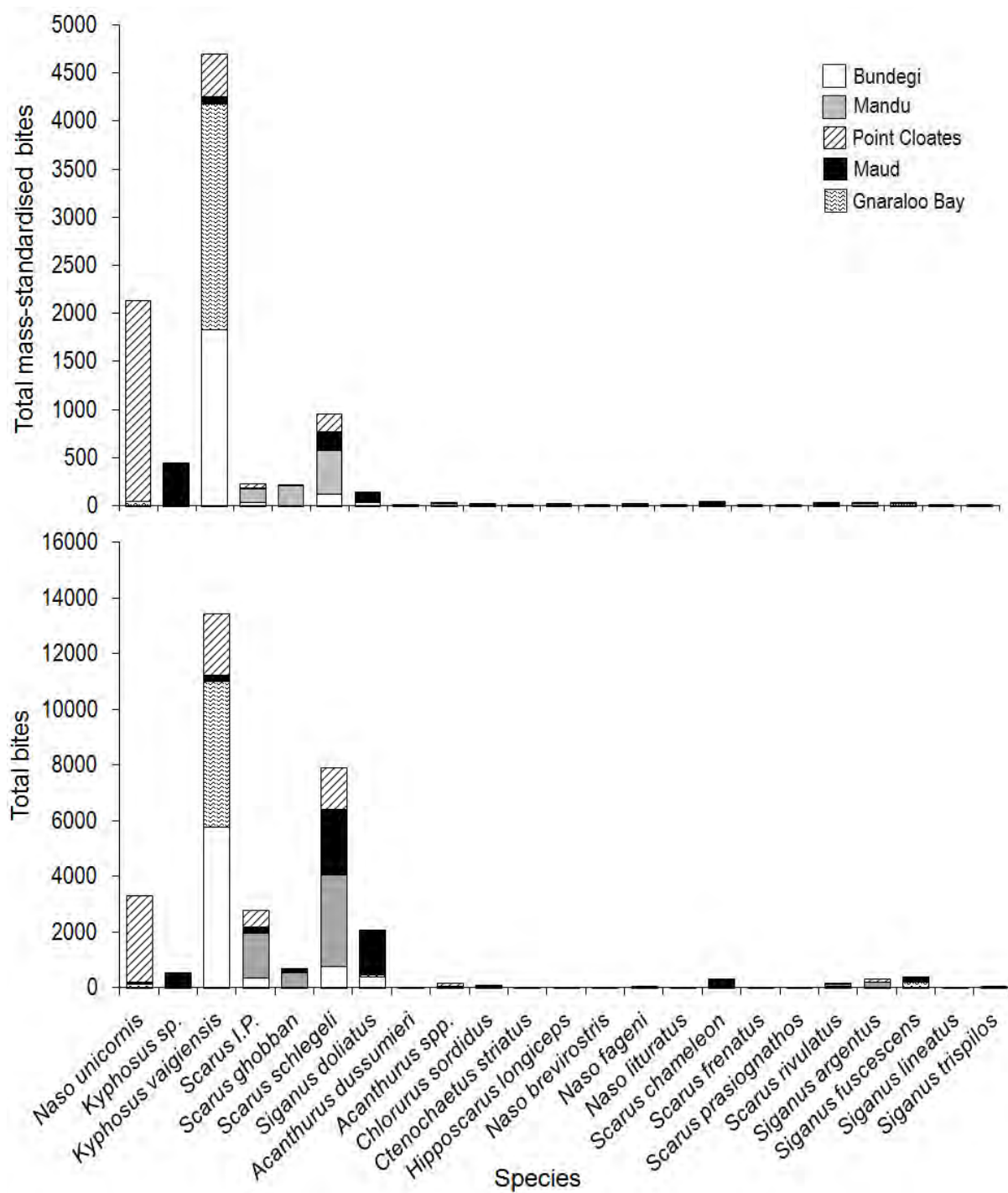


Figure 4.2. The total number of mass-standardised bites, and raw bites, taken by fishes on the transplanted *Sargassum* assays across five regions of the Ningaloo Reef.

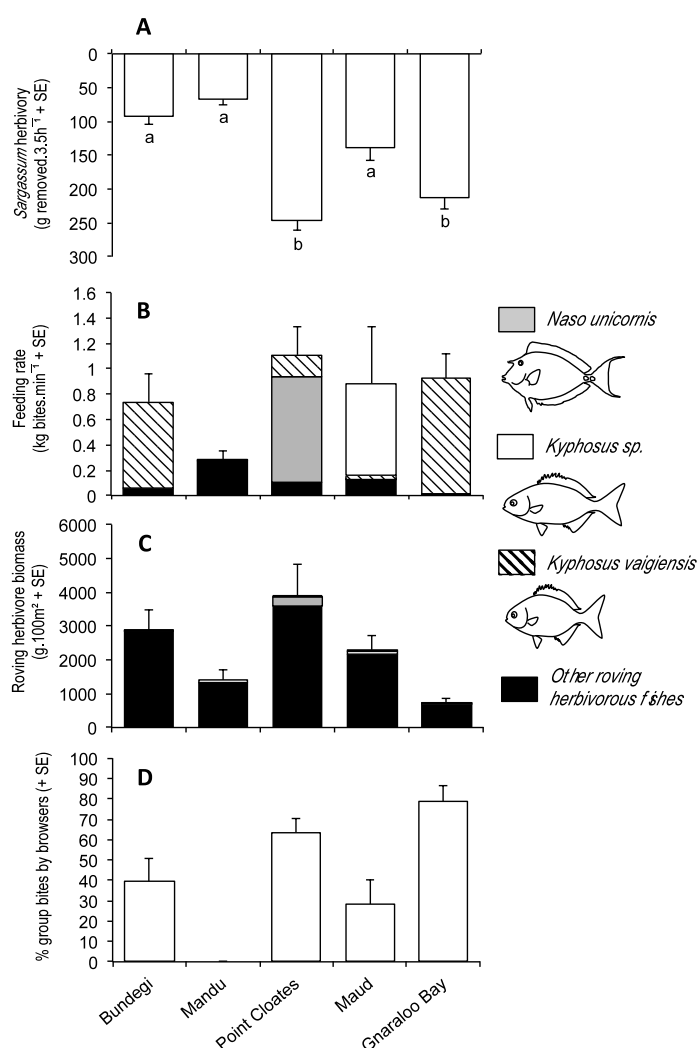


Figure 4.3. Variation across the five broad-scale regions of Ningaloo Reef for: **A)** herbivory on *Sargassum* by fishes. Columns represent mean (+ SE) biomass reduction from 36 replicate *Sargassum* assays per region. Regional means sharing the same letter do not statistically differ (SNK post-hoc analysis); **B)** Mean (+ SE) feeding rate (kg bites.min⁻¹) of herbivorous fishes recorded from video observations ($n = 12$ filmed replicates per region); **C)** Mean (+ SE) biomass (g.100m²) of the dominant macroalgal browsers (*Naso unicornis*, *Kyphosus sp.* and *K. vaigiensis*) and other roving herbivores (29 species pooled) encompassing the transplant experiment area ($n = 12$ UVCs per region); and **D)** Mean (+ SE) proportion of bites taken by *N. unicornis*, *Kyphosus sp.* and *K. vaigiensis* whilst part of a feeding group association ($n = 12$ filmed replicates per region).

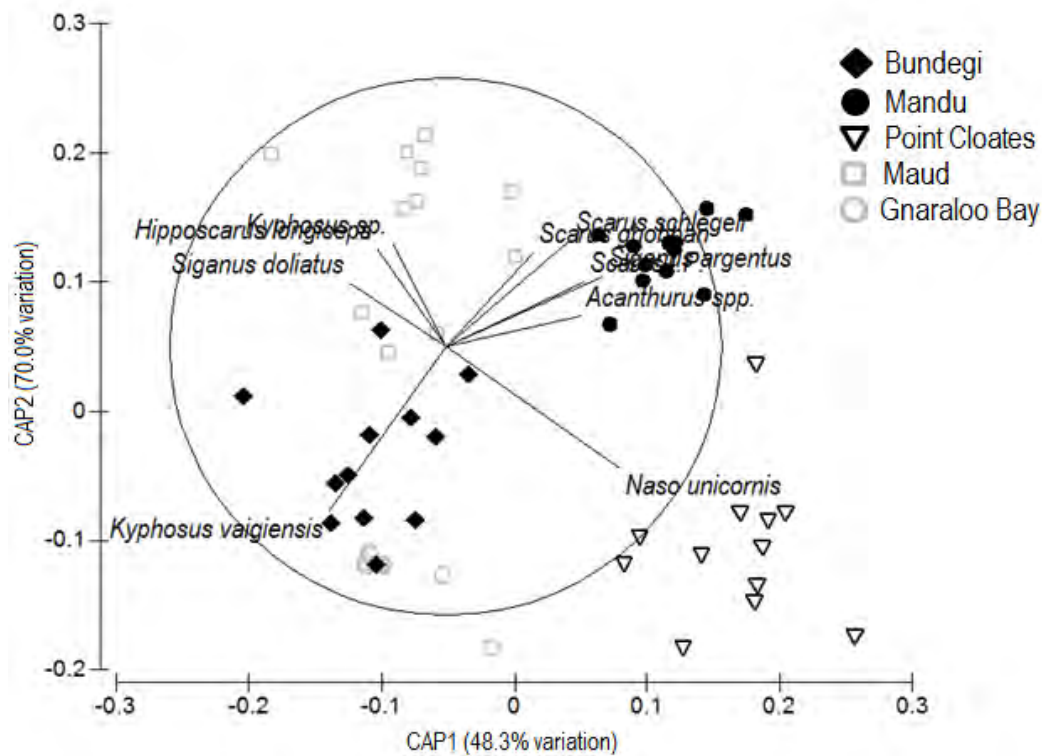


Figure 4.4. Canonical analysis of principal coordinates (CAP) ordination based on Bray-Curtis similarities between bite rates ($\text{kg bites} \cdot \text{min}^{-1}$) of 23 feeding species recorded during video observations of transplanted *Sargassum* assays across five regions of the Ningaloo Reef. Overlaid is a plot of species bite-rate correlations (Pearson correlation coefficient set at > 0.4) with the canonical axes. Data points represent bite-rates observed from a filmed replicate ($n=12$ per region). All data were square root transformed.

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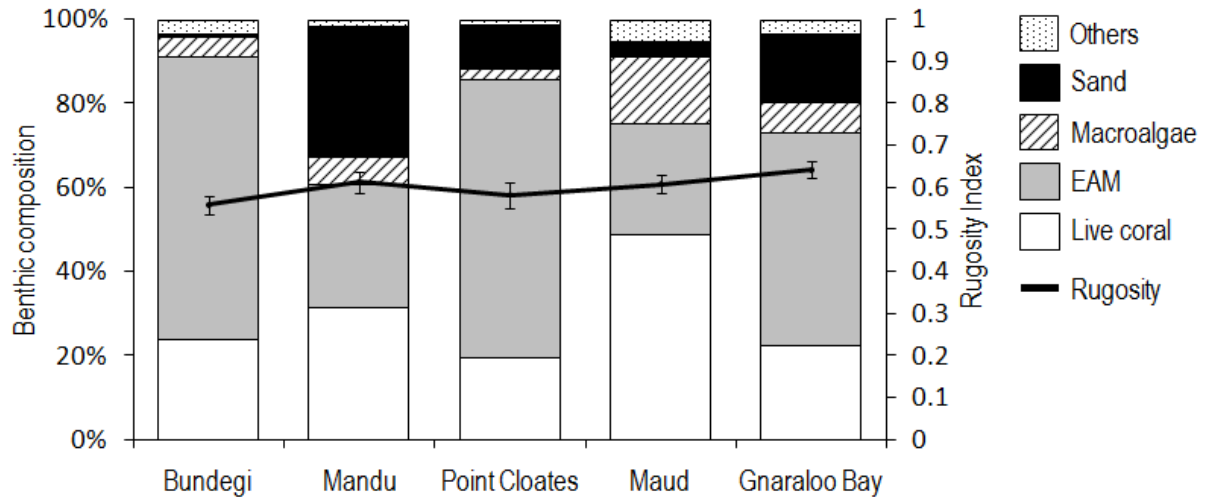


Figure 4.5. Rugosity Index and proportional cover of the dominant benthic habitat categories across each broad-scale region of Ningaloo Reef. Solid line represents mean Rugosity Index (\pm SE). Each category within the regional columns represents the mean percent cover determined from 180 photo-quadrats across three replicate reef-flat sites. The category 'Others' includes the pooled percentage contributions to the benthos cover by the categories: crustose coralline algae, dead coral and damselfish territory.

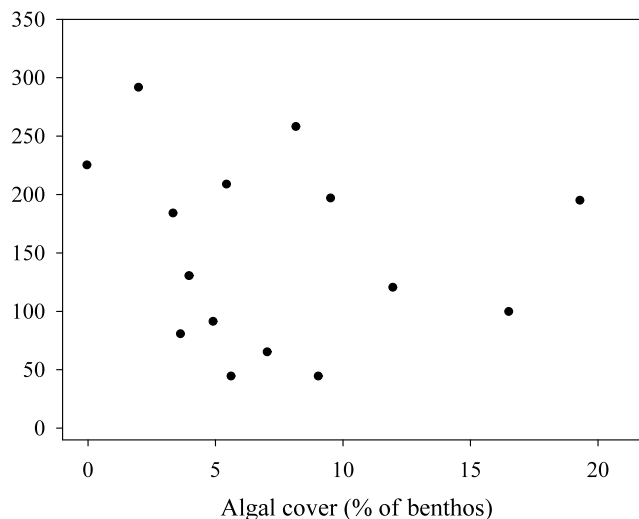


Figure 4.6. Non-significant relationship between *Sargassum* herbivory and the proportion of naturally occurring macroalgae cover within transplant areas (ANOVA, $F = 1.3019$, $p = 0.3078$). Data points represent mean values for each reef-flat site.

Table 4.1. Results of ANOVA on biomass removed from *Sargassum* tethers by fishes, testing for differences between Regions (50-300 km), among Sites (<1 km) and Days within each of these spatial scales. Parentheses indicate the levels each of the factors is nested within. Bold figures indicate significance ($p < 0.05$).

Source of variation	df	MS	F	p
Region	4	209004.95	10.45	0.001
Site (Region)	10	20003.06	0.60	0.791
Day (Region x Site)	15	33406.83	7.56	< 0.001
Residual	150	4420.04		

Table 4.2. Hierarchical ANOVA on the total number of bites taken by all fishes of the filmed *Sargassum* assays, testing for differences between Regions (50-300 km), among Sites (<1 km) and Days within these spatial scales. Analyses were based on square-root transformed bite count data. Parentheses indicate the levels each of the factors is nested within and bold figures indicate significance ($p < 0.05$).

Source of variation	df	MS	F	p
Region	4	54.71	0.51	0.732
Site (Region)	10	107.97	0.70	0.708
Day (Region x Site)	15	153.50	2.85	0.007
Residual	30	134.85		

Table 4.3. Multiple regression analysis examining the relationship between feeding species bite rates ($\text{kg bites} \cdot \text{min}^{-1}$) recorded from video observations and the corresponding biomass removed from filmed *Sargassum* assays. Analyses were based on square-root transformed feeding rate data. Overall model Adjusted $R^2 = 0.73$ ($R^2 = 0.77$), $F = 16.49$, $p < 0.001$. Significant ($p < 0.05$) variables are highlighted in bold text.

	Total bites	Coeffi cient	SE	t	p
Macroalgae browsers					
<i>Naso unicornis</i>	3299	192.28	25.19	7.63	< 0.001
<i>Kyphosus</i> sp.	565	151.25	22.56	6.70	< 0.001
<i>Kyphosus vaigiensis</i>	13443	157.90	20.19	7.82	< 0.001
Grazers					
<i>Scarus ghobban</i>	647	76.97	104.92	0.73	0.466
<i>Scarus l.P.</i>	2793	-1.96	126.23	0.02	0.987
<i>Scarus schlegeli</i>	7922	42.47	63.52	0.67	0.507
<i>Siganus doliatus</i>	2065	-107.95	103.37	1.04	0.301
Other broad taxa (pooled)					
Other Acanthurids	228	-12.97	196.21	0.07	0.947
Other Scarids	655	-61.49	181.00	0.34	0.735
Other Siganids	777	65.62	162.42	0.40	0.688

Table 4.4. Results of PERMANOVAs examining variation in bite rates (kg bites.min^{-1}) of **A)** all feeding species, and **B)** the dominant macroalgal browsers separately, across Regions (50-300 km), Sites (<1 km) and Days within each of these spatial scales. Parentheses indicate the levels each of the factors is nested within. The analyses were conducted using Bray-Curtis dissimilarities (for all feeding species, A) or based on Euclidean distances (macroalgal browsers individually, B) using square-root transformed bite rate data. P-values were obtained using 4999 unrestricted random permutations. Bold values indicate significance ($p < 0.05$).

		Source of variation	df	MS	Pseudo - F	p
A)	All species	Region	4	22863.00	9.00	< 0.001
		Site (Region)	10	2539.30	1.00	0.476
		Day (Region x Site)	15	2530.70	2.53	< 0.001
		Residual	150	998.75		
B)	Naso unicornis	Region	4	1.57	179.23	0.012
		Site (Region)	10	0.01	0.07	1.000
		Day (Region x Site)	15	0.12	16.94	< 0.001
		Residual	30	0.01		
	Kyphosus vaigiensis	Region	4	1.68	7.13	0.007
		Site (Region)	10	0.24	1.34	0.287
		Day (Region x Site)	15	0.18	5.97	< 0.001
		Residual	30	0.03		
	Kyphosus sp.	Region	4	0.45	2.17	0.011
		Site (Region)	10	0.21	0.75	1.000
		Day (Region x Site)	15	0.28	47.49	0.002
		Residual	30	0.01		

Table 4.5. Multiple regression analysis examining the relationship between group feeding of macroalgal browsers (% bites as a group) and *Sargassum* removed from filmed replicates. Percentage feeding data were arcsine transformed for the analysis. Overall model Adjusted $R^2 = 0.65$ (Multiple- $R^2 = 0.66$), $F = 36.6$, $p < 0.001$. Significant ($p < 0.05$) variables are highlighted in bold text.

Species	Coefficient	SE	t	p
<i>Naso unicornis</i>	125.10	19.99	6.25	< 0.001
<i>Kyphosus</i> sp.	180.55	31.08	5.81	< 0.001
<i>Kyphosus vaigiensis</i>	118.45	17.05	6.94	< 0.001

Table 4.6. Hierarchical ANOVA on total herbivorous fish (all roving species pooled) biomass ($\text{g} \cdot 100\text{m}^{-2}$), testing for differences between Regions (50-300 km), among Sites (<1 km) and Days within each of these spatial scales. Analyses were based on square-root transformed biomass data. Parentheses indicate the levels each of the factors is nested within and bold figures indicate significance ($p < 0.05$).

Source of variation	df	MS	F	p
Region	4	2038.80	3.78	0.040
Site (Region)	10	539.38	1.65	0.184
Day (Region x Site)	15	326.99	2.42	0.019
Residual	30	134.85		

Table 4.7. Relationship between roving herbivorous fish biomass (g.100m²) and the biomass removed from transplanted *Sargassum* by fishes across all regions of the Ningaloo Reef. Fish biomass data were square-root transformed and bold figures indicate significance ($p < 0.05$). The regional mean (\pm SE) biomass for each group of fishes is also given.

Species	Mean regional biomass (g. 100m ²)	Correlation coefficient	R ²	p
All roving herbivorous fishes (32 species pooled)	2211.67 (\pm 282.71)	-0.03	0.00	0.887
Macroalgal browsers (3 species pooled)	115.23 (\pm 21.42)	0.19	0.03	0.328
<i>Naso unicornis</i>	100.81 (\pm 20.35)	0.24	0.06	0.201
<i>Kyphosus vaigiensis</i>	14.42 (\pm 6.10)	-0.03	0.00	0.880
<i>Kyphosus</i> sp.	Species not observed during any UVC			
<i>Scarus ghobban</i>	95.35 (\pm 20.48)	-0.37	0.13	0.047
<i>Scarus schlegeli</i>	48.56 (\pm 7.78)	-0.23	0.05	0.228
<i>Scarus</i> l.P.	129.63 (\pm 24.60)	-0.23	0.05	0.225
<i>Siganus doliatus</i>	38.86 (\pm 12.82)	-0.30	0.09	0.113

Table 4.8. Multiple one-way ANOVAs examining variation in the major benthic categories among regions. All benthic cover data was square root arcsine (%) transformed and rugosity data were arcsine (proportion) transformed. Bold figures indicate significant ($p < 0.05$) values.

Benthic category	Source of variation	df	MS	F	p
Live coral	Region	4	173.30	3.12	0.065
	Residual	10			
EAM	Region	4	405.09	25.84	<0.001
	Residual	10			
Macroalgae	Region	4	102.26	6.16	0.009
	Residual	10			
Sand	Region	4	423.86	26.12	<0.001
	Residual	10			
Rugosity Index	Region	4	0.06	2.19	0.142
	Residual	10			

Discussion

Our study demonstrated a high level of variability in rates of herbivory by fishes, and in the identity of the main herbivores, across the entire spatial extent encompassed by a fringing coral-reef ecosystem, the Ningaloo Reef (ca. 300 km). We also identified that it is the variation in feeding of a few species within multi-species feeding assemblages that drives the observed patterns of macroalgal removal. Despite the presence of at least 32 roving herbivorous fish species (as determined through UVCs in this study), consumption of tethered *Sargassum* was largely due to three fish species, namely *Naso unicornis* (Acanthuridae), *Kyphosus* sp. and *K. vaigiensis* (Kyphosidae). The dominance of *N. unicornis* and kyphosids in this west-continental coral-reef system supports and extends on findings in Ningaloo Reef (Chapter 3) and previous findings from inner- and mid-shelf GBR, which have also identified that a subset of the species present are usually responsible for a disproportionate amount of consumption, with the identity of these consumers varying from place to place (Bellwood et al. 2006b, Mantyka and Bellwood 2007a, Fox and Bellwood 2008, Cvitanovic and Bellwood 2009, Hoey and Bellwood 2009, Bennett and Bellwood 2011).

Peterson et al. (1998) hypothesised that when there are several species performing similar functional roles within a single system, they may provide a mutual reinforcement to one another that contributes to the resilience to disturbances. In the present study, three species, *Naso unicornis*, *Kyphosus* sp. and *K. vaigiensis* demonstrated the capacity to consume tethered *Sargassum* across different regions of Ningaloo Reef, indicating the potential for some, albeit limited, functional redundancy within this system. This disproportionate role of a select few species within the herbivorous guild to remove this dominant alga appears to be a constant feature elsewhere, regardless of the spatial resolution being examined (cf. Cvitanovic and Bellwood 2009, Hoey and Bellwood 2009, Bennett and Bellwood 2011). The stability of these species is, therefore, likely to be critical to the resilience of coral-reef systems of Australia, and perhaps elsewhere. The failure of many reefs to recover following perturbations, while undergoing a transition from coral- to macroalgal-dominated states, may be partially due to the absence of, or limited functional redundancy within, such critical functional groups (Bellwood et al. 2004).

Other roving herbivorous species played only a minor role in the removal of macroalgal biomass, despite high bite counts by several species, including the parrotfishes *Scarus* I.P., *S. schlegeli* and *S. ghobban*, and the rabbitfish *Siganus doliatus*. We observed these fishes taking small, rapid bites when feeding (Michael *unpubl. data*), resulting in little apparent contribution to the algal biomass loss. These findings are consistent with other studies, which have also described the functional inability of these groups of grazing fishes to rapidly remove erect macroalgae (e.g. Bellwood et al. 2006b, Fox and Bellwood 2008, Fox et al. 2009). In contrast, the success of *N. unicornis* and kyphosids in consuming tethered *Sargassum* is not surprising, since these fishes are among a small group of coral-reef fishes that are morphologically and physiologically capable of consuming some fucoid brown macroalgae (Clements and Choat 1997, Choat et al. 2004, Crossman et al. 2005).

The variable role of fishes and their relative importance in mediating coral-reef algal assemblages is recognised to be dynamic, but the variability in our study raises the question as to why the identity of the main herbivorous species, and the subsequent levels of quantified herbivory differ markedly within the same habitat types across broad-scale regions of a single coral-reef system. Such variation may partially be the result of variation in macroalgal browser distribution, the relative abundance, susceptibility and palatability of the tethered *Sargassum*, differences in structural complexity of the transplant habitat and differences in browser feeding behaviour among regions. These options are discussed below.

The removal rate of *Sargassum* was not related to the biomass of macroalgal browsers observed in UVC, both individually and collectively. One of the main consumers of tethered

Sargassum, *Kyphosus* sp., was never detected during visual censuses, yet in the absence of divers (as shown by video) they fed in groups of greater than 15 individuals and had a dramatic impact on the *Sargassum* tethers. Conversely, although *N. unicornis* was observed on UVC in Bundegi and Mandu, it did not feed in these regions at all. Such difficulties in predicting ecosystem function based on presence has been highlighted in similar observational-based studies, which have also failed to detect the key drivers of macroalgal herbivory based on underwater visual observations alone (Fox and Bellwood 2008, Cvitanovic and Bellwood 2009, Hoey and Bellwood 2009). Importantly, these results highlight that the species critical to the functioning and resilience of reef systems against a change in macroalgal abundance may go unnoticed through the single-handed use of underwater visual observations of fish communities. This increased awareness of observer-based limitations has reinforced the importance of the recent novel direction in herbivory studies which aim to directly quantify species-specific impacts, rather than the use of inference (e.g. Bellwood et al. 2006b, Mantyka and Bellwood 2007b, Burkepile and Hay 2008, Fox and Bellwood 2008, Cvitanovic and Bellwood 2009, Hoey and Bellwood 2009, Bennett and Bellwood 2011, Chapter 3).

Variation in consumption rates of *Sargassum* tethers may be the result of regional differences in the abundance, susceptibility and palatability of the transplanted macroalgae. Removal rates of the tethers by fishes may be partially influenced by the abundance and relative palatability of resident algal communities within the local area (Cvitanovic and Hoey 2010, Hoey and Bellwood 2010a), as well as the density of the tethered algae itself (Hoey and Bellwood 2011). Regional cover of resident macroalgae was significantly higher in Maud ($15 \pm 1.5\%$) (Figure 4.5 & Table 4.6), a pattern driven by a seasonal patchy understory growth of predominantly *Turbinaria* which is consumed by *N. unicornis* (Choat et al. 2002) and *K. vaigiensis* (Clements and Choat 1997) elsewhere. Despite this availability of an alternative food source, there was no distinct relationship between the abundance of macroalgae and rates of *Sargassum* removal in this study (Figure 4.6). In terms of palatability, we minimised potential variation of this trait by using a single algal species in a similar condition (*S. myriocystum* without visible large epiphytes) for all tethers. Although intra-specific variation in nutritional traits and/or chemical defences among local populations is possible and has been reported to influence herbivory by invertebrates in a temperate system (Taylor et al. 2003), secondary metabolite concentrations are relatively lower in tropical species of *Sargassum* (Steinberg 1986), often making them ineffective in deterring many tropical herbivorous fishes (Steinberg and Paul 1990, Steinberg et al. 1991). Moreover, the conclusion that variation in chemical or physical deterrence is unlikely to explain variation in grazing rates is supported by the fact that the *Sargassum* used at both Gnaraloo Bay and Maud was collected from the same meadow, yet its consumption rates differed significantly between these two regions.

Feeding rates by herbivorous fishes have been shown to be influenced by the provision of benthic structural complexity (Fox and Bellwood 2007, Vergés et al. Chapter 2) and have been suggested to partly explain the different macroalgal consumption rates by browsers across regions within the GBR (Bennett and Bellwood *In press*). Macrophytes growing in refuge areas from intense fish grazing (such as the *Sargassum* collected from unstructured lagoon habitats in this study) are generally poorly defended against herbivory, and are rapidly consumed when moved to a nearby structured habitat with a higher abundance of herbivorous fishes (Hay 1981a, Lewis 1986). However, in our study, we tethered *Sargassum* to similarly structured reef-flat substrata in all regions (Figure 4.5), thereby minimising any regional variation in refuge availability or accessibility to the macroalgal tethers by fishes.

An alternative explanation for the variation in feeding rates may relate to differences in feeding behaviour of the browsing species observed in the present study. We observed a large portion of the bites by the dominant macroalgal browsers, *N. unicornis*, *Kyphosus* sp. and *K. vaigiensis*, occurring whilst part of monospecific or multi-species foraging associations, and therefore, detected a significant positive relationship between this group feeding activity and *Sargassum* removal efficiency. Such group foraging may enhance the ability of some individuals to locate and consume resources more rapidly than when alone, with successful foragers attracting other group members through behavioural cues

associated with successful foraging (Baird et al. 1991, Lukoschek and McCormick 2000). This general foraging theory appears to be consistent with the feeding behaviour of fishes observed in our study, where individuals often made several passes at the filmed tethered *Sargassum* before being joined by conspecifics for group feeding. Group feeding appears to be a behaviour exhibited by macroalgal browsers elsewhere (e.g. *Siganus canaliculatus*, Fox and Bellwood 2008; *N. unicornis*, Hoey and Bellwood 2009), as it probably serves as predator protection (Ogden and Lobel 1978) or a strategy to overcome the territorial defence of algal patches by territory holding species (Robertson et al. 1979, Foster 1985). Several authors have described the greater foraging rates of fishes when feeding in a group compared to when alone (Robertson et al. 1979, Foster 1985, Reinthal and Lewis 1986, Wolf 1987), however, to the best of our knowledge, this study represents the first attempt to directly quantify the influence of group feeding by fishes on *Sargassum* removal efficiency in a coral-reef system. In our study, this feeding behaviour appeared to have influenced the feeding interactions within and among species and, therefore, the variability in species-specific feeding rates and herbivory being quantified. For example, the *Sargassum* mass loss was nearly two and a half times greater in Gnaraloo Bay than in Bundegi; yet bite rates of the dominant browser *K. vaigiensis* did not differ between the two regions. In this case, the kyphosids in Bundegi took more than half the total bites whilst feeding as individuals, whereas, schools of up to 15 simultaneously feeding fishes took on average 80% of the bites in Gnaraloo Bay. An alternative, that is not mutually exclusive, is that variation in territorial behaviour may also explain some of the variation in algal biomass loss. In some sites, aggressive territorial behaviour was displayed by juvenile *K. vaigiensis* as they often chased other herbivorous fishes from the filmed tethers during feeding (Michael *unpubl. data*). Such territory-holding behaviour has been reported for kyphosids elsewhere (Hamilton and Dill 2003), and further highlights the need to consider the behavioural aspects of species interactions when distinguishing the potential impact of a species on ecosystem processes. The extent to which these feeding behaviours exclude other fishes or alter efficiency in macroalgal consumption is partially unclear, but is likely to explain some of the variability that occurs across space and time in this study.

Typically, nearshore coral reefs are faced with the most imminent predisposition to change due to their close proximity to increasing human use and terrestrial influences (e.g. McCulloch et al. 2003). However, the Ningaloo Reef represents a unique coral-reef system, which unlike many of its counterparts, is relatively unaffected by anthropogenic pressures and receives little input from terrestrial sources (Cassata and Collins 2008). The results of our study, therefore, may provide a useful baseline for our understanding of the potential role of macroalgal browsers in a relatively intact nearshore coral-reef system. Given the unprecedented worldwide decline in coral-reef health in recent decades (Gardner et al. 2003, Pandolfi et al. 2005, Bruno and Selig 2007), and subsequent urgent calls for process-oriented research and management (Hughes et al. 2003, 2005, Folke et al. 2004), understanding variation in mechanisms such as herbivory that promote the resilience of coral reefs is essential. We are currently moving beyond just recognising the importance of the entire herbivorous guild in shaping benthic communities, to acknowledging the species-specific quantitative nature of these algal-herbivore interactions. In this study, the use of remote video cameras has provided an insight into the highly variable patterns of macroalgal herbivory and the key drivers that are likely to play an integral role in maintaining a healthy balance between coral and macroalgae across multiple spatial scales of the Ningaloo Reef.

CHAPTER 5. Variability in the food sources of herbivorous invertebrates and fishes in a coral-reef system: a stable isotope approach

Glenn Hyndes, Adriana Vergés and Mathew Vanderklift

Introduction

Herbivores in coral-reef systems play an integral role in removing macroalgae that can otherwise outcompete corals (Hughes et al. 2003, Bellwood et al. 2004). Altering the herbivore-algae balance of interactions through disturbance, such as overfishing (Jackson et al. 2001) or disease (Hughes 1994), can result in a shift from a coral- to macroalgae-dominated state (Bellwood et al. 2006c, Hughes et al. 2007). The high diversity of herbivores, particularly fish, in coral-reef systems (Clements et al. 2009) has produced considerable debate regarding functional redundancy within this group in terms of maintaining the balance between corals and macroalgae (Bellwood et al. 2003, Fox et al. 2009).

The functional roles within “nominally” herbivorous fishes can differ markedly. Roving herbivorous fishes can be broadly classified into two functional groups: grazers and browsers (Hoey & Bellwood 2010a). The grazers include scraping and excavating parrotfish (Labridae), which feed on the epilithic algal matrix (EAM) and algal turf (sensu Wilson et al. 2003), while browsers (mostly members of Kyphosidae and some Acanthuridae) remove erect, tough macroalgae from the reef (Bellwood et al. 2006a). This functional group approach has provided insights into the role of nominally herbivorous fishes in maintaining coral-reef ecosystems (Hughes et al. 2003, Bellwood et al. 2004). However, it has been argued that a greater focus should be placed at the species level (Clements et al. 2009). Different species may share similar morphologies and feeding behaviours, but they can exhibit differences in their nutrient intake and assimilation (Bellwood et al. 2003, Crossman et al. 2005) and grazing impacts may also differ among species (Fox & Bellwood 2007). Thus, there is a need to understand the relative roles of herbivores at the species level to explain interactions between consumers and their food sources within coral-reef ecosystems.

Knowledge on the role of “nominally” herbivorous fishes in coral-reef systems has generally been gained through two distinct approaches. Firstly, an understanding of herbivore nutrition has been gained through examination of gut contents and biomarker (e.g. lipids, carbohydrates and amino acids) composition of the digestive tract and tissue of fishes (e.g. Wilson et al. 2001, Choat et al. 2002, Choat et al. 2004, Crossman et al. 2005). The use of lipids particularly has provided insights into the importance of detritus and zooplankton in the diets of a range of “nominally” herbivorous fishes (Wilson et al. 2001, Crossman et al. 2005). Secondly, an understanding of the impact of grazing on the algal assemblages has been gained through macroalgal bioassays experiments (Fox & Bellwood 2007, Hoey & Bellwood 2010a). This approach has allowed differences in grazing rates on macroalgae across species, regions and habitats to be determined (Fox & Bellwood 2007, Hoey & Bellwood 2010a, Vergés et al. 2011, Bennett & Bellwood 2011), regardless of whether nutrients from the algae are assimilated by the grazers and incorporated into the food web. Surprisingly, few studies have attempted to provide an understanding of the integration of food sources by these herbivores.

Stable isotopes provide an alternative and complementary tool to characterise food webs in marine ecosystems, and have been valuable in examining food-web interactions in several marine environments (e.g. Moncreiff & Sullivan 2001, Adin & Riera 2003, Melville & Connolly 2003, Hyndes & Lavery 2005). In tropical environments, stable isotopes have provided an understanding of food web interactions in a mosaic of habitats within coral-reef landscapes

(e.g. Yamamuro et al. 1995, Nagelkerken et al. 2006, Nyunja et al. 2009) as well as providing insights on specific trophic level and ontogenetic shifts in diets of coral-reef fishes (e.g. de la Moriniere et al. 2003, Carassou et al. 2008, Nakamura et al. 2008, Greenwood et al. 2010). However, our understanding of the variability in food sources among assimilated by fishes broad-scale regions or coral habitats is limited. Grazing rates by herbivorous species in coral-reef systems can vary over large spatial scales (Bennett & Bellwood 2011, Vergés et al. In review), but these algal-assay studies provide little insight into the variation of food-source integration into the coral-reef food webs. Yet, the importance of various food sources has been shown through stable isotopes to vary over small (e.g. habitat) and large (regional scales) for a range of consumers in other marine systems (Wing et al. 2008, Vanderklift & Wernberg 2010).

In this study, we hypothesised that the food sources would vary among species within the two functional groups of nominally herbivorous fish species, namely scrapers and browsers, as well as herbivorous invertebrate species in a coral-reef system. Furthermore, we predicted that the food sources would vary among regions (over a spatial scale of 10s kilometres) and among habitats (over a cross-shelf spatial scale of 100s metres) within each species. We have used dual stable isotopes ($\delta^{15}\text{N}$ and $\delta^{13}\text{C}$) to infer dietary shifts among and within species at Ningaloo Reef on the west coast of Australia, and in doing so, examined the spatial shifts in $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ for a range of potential dietary sources (autotrophs) and herbivorous fish and invertebrate species. This has allowed us to determine, through mixing model analyses of stable isotopes, whether the assimilation of food sources differ among and within herbivorous species.

Materials and methods

Study area and sample collection

This study was conducted on the Ningaloo Reef, a fringing coral-reef system extending ~290 km along the north-west coast of Western Australia. Regional comparisons within reef-flat habitat were made among three Sanctuary Zones where no fishing activities are allowed (Bundegi 21°51'S, 114°10'E; Mandu 22°05'S, 113°52'E; Maud 23°05'S, 113°44'E;), while habitat comparisons were made among outer-reef, reef-flat and lagoon habitats within the Mandu Sanctuary Zone (Figure 5.1). All sampling was undertaken at depths between 1 and 6 m in each habitat/region over two months (July - September 2008) to minimise temporal variations in isotopic signatures (Owens 1987). The coral-dominated reef-flat habitat was chosen for regional comparisons because this habitat displays the highest levels of herbivory and herbivore biomass (Chapter 2).

Within each region/habitat, 3-5 replicate samples of benthic primary producers and herbivorous invertebrates were haphazardly collected by hand by divers over distances of metres to 100s of metres. Samples of Epilythic Algal Matrix (EAM) were obtained by collecting boulders and pieces of dead coral and gently brushing off all loose sediment and detritus particles with a soft brush. These aqueous EAM samples were filtered through a 125 μm sieve and allowed to settle for 1-2 hours before excess water was decanted. In each region/habitat, 3-5 individuals of two gastropod species and one echinoderm species were collected by hand, and 14 nominally herbivorous fish species were collected by spear fishing. Since Kyphosidae species were often difficult to distinguish, they have been pooled for this study. Muscle tissue was taken from the foot of gastropods, the Aristotle's lantern of sea urchins, and the dorsal body of fish. Samples were then frozen immediately after collection and processing and stored at -20°C until laboratory analysis. Prior to analysis, macrophytes were rinsed with seawater, and cleaned of epiphytes where necessary.

Sampling resulted in three species of invertebrates and 14 species of nominally herbivorous fishes, including 8 species designated as scrapers and six as browsers (Table 5.1).

Stable isotope analysis

All samples were freeze-dried, homogenized to a fine powder using a ball mill and weighed into tin capsules. For those samples requiring removal of inorganic carbon (e.g. calcareous algae, EAM), subsamples were weighed into silver capsules and acid-treated by adding drops of 1N HCl until effervescence ceased (Boutton 1991) before $\delta^{13}\text{C}$ analyses. All samples were analysed for stable isotopes by firstly combusting samples in an elemental analyser (ANCA-GSL, Europa, Crewe, United Kingdom) and purifying them by gas chromatography. Nitrogen and carbon elemental composition and stable isotope ratios were then determined using continuous flow isotope ratio mass spectrometry (20-20 IRMS, Europa, Crewe, United Kingdom). For calibration, samples were interspersed with reference materials of known elemental composition and stable isotope ratios. Reference had previously been calibrated against International Atomic Energy Agency (IAEA) or National Institute of Standards and Technology (NIST) reference materials with a precision (1 SD from ~10 samples) of $< 0.1\text{‰}$. Results are reported relative to Vienna PeeDee Belemnite (V-PDB) for $\delta^{13}\text{C}$ and atmospheric N_2 for $\delta^{15}\text{N}$, and expressed in δ notation as: $\delta X (\text{‰}) = ((R_{\text{sample}}/R_{\text{standard}}) - 1) \times 1000$, where $X = ^{13}\text{C}$ or ^{15}N , and $R = ^{13}\text{C}:^{12}\text{C}$ or $^{15}\text{N}:^{14}\text{N}$.

Data analyses

Statistical and mixing modelling analyses were conducted for each species/group that was represented in at least 2 regions or 2 habitats, and by at least 3 replicate samples from each region or habitat. One-way univariate PERMANOVA was used to test for the magnitude and significance of variation among regions or habitats in $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ based on Euclidean distance-based linear models with significance tests by permutation using PERMANOVA+ add-on package for PRIMER v6 (Anderson 2001, McArdle & Anderson 2001, Clarke & Gorley 2006, Anderson et al. 2008b). Euclidean distance measures, in these univariate cases, yield estimates of sums of squares equivalent to parametric ANOVA, but the use of permutation allows for significance to be tested without the assumption of normality. PERMDISP (equivalent to Levene's test for heterogeneity of variances in the univariate tests (Anderson et al. 2008b) was used to test for homogeneity of dispersion. We have focused on the relative magnitude of effect (the variance component of each factor, divided by the sum of all variance components), which unlike P values, does not depend directly on the degrees of freedom (Graham & Edwards 2001). Any negative variance components were set to zero following the pooling procedure outlined by Graham and Edwards (2001).

Mixing model analyses were conducted on dual isotopes ($\delta^{15}\text{N}$ and $\delta^{13}\text{C}$) using MixSIR (V 1.0.4), a Bayesian stable isotope mixing model incorporating variability (Moore and Semmens 2008) to examine the potential dietary contributions of herbivorous invertebrate and fish species in each region for the reef-flat habitat and in each habitat at Mandu. Sources for each consumer species were selected from the list used for statistical analyses (above), based on whether they were relatively abundant in each region/habitat (Vanderklift and Babcock, unpublished data). Where the mean $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ for species of sources within a functional algal group (e.g. large brown macroalgae) were within 1‰ in each region/habitat, the replicate data were pooled for mixing model analyses, as they were considered to be similar and pooling would reduce any ambiguity associated with stable isotope results. Based on published literature, discrimination levels (Δ) of 2.4‰ (± 1.8 SD) and 0.6‰ (± 0.2 SD) were used for $\delta^{15}\text{N}$ (McCutchan et al. 2003) and $\delta^{13}\text{C}$ (DeNiro & Epstein 1981), respectively, in the mixing model for invertebrates, and 4.8‰ (± 1.3 SD) and 1.8‰ (± 0.2 SD) for $\delta^{15}\text{N}$ (Mill et al. 2007) and $\delta^{13}\text{C}$ (Caut et al. 2009), respectively, for nominally herbivorous fish. Sufficient iterations were carried out to ensure at least 1000 posterior draws in the final output for each mixing model run. The distributions of feasible solutions are presented by providing the 5th, 25th, 50th (median), 75th and 95th percentiles for each potential source contribution.

Results

Species and regional comparisons

All species of brown algae exhibited relatively low variability in $\delta^{15}\text{N}$, as highlighted by the variance components, though variability was greatest at the region level particularly for *Turbinaria ornata* (Table 5.2, Figure 5.2). In comparison, *Sargassum oligocystum* showed far higher variability for $\delta^{13}\text{C}$, which was mainly explained by within-region differences, while *Lobophora variegata* showed greater regional variation in this isotope. Again, the variance components of $\delta^{15}\text{N}$ were low for red algae, but were proportionately higher across regions in the case of foliose alga *Hypnea pannosa* and crustose coralline algae, and within region for the foliose algae *Acanthophora spicifera* and *Portiera hornemanii* and articulated coralline algae (Table 5.2, Figure 5.2). Variability of $\delta^{13}\text{C}$ was often greater than that of $\delta^{15}\text{N}$ for red algae, with the greatest variation exhibited across regions for *A. spicifera*, articulated coralline algae and crustose coralline algae. In comparison, all the variation was explained by within-region differences for *H. pannosa* and *P. hornemanii*. Variation in both $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ was relatively small for the seagrass *Halophila* sp., but was apportioned mainly by region and within region for the respective isotopes. Variance components of $\delta^{13}\text{C}$ were high for EAM, which exhibited greatest variance within region, while cyanobacterial matt exhibited the highest $\delta^{15}\text{N}$ variance among regions (Table 5.2, Figure 5.2).

All three herbivorous invertebrate species exhibited relatively low variance components for $\delta^{15}\text{N}$ (Table 4.2). Variability was higher within regions for this isotope in the gastropod *Tectus pyramis* and the urchin *Echinometra mathaei* (Table 5.2, Figure 5.2). Variance was far greater in $\delta^{13}\text{C}$ than $\delta^{15}\text{N}$ for all invertebrate species, with the two gastropod species displaying greater variance than the urchin. *Tectus pyramis* exhibited greatest $\delta^{13}\text{C}$ variation between regions (Table 5.2, Figure 5.2).

Similar to invertebrates, the variance components of $\delta^{15}\text{N}$ were generally low for all fish species. However, *Kyphosus* spp. displayed far greater variation in $\delta^{15}\text{N}$, which was explained by within region differences (Table 5.2, Figure 5.2). In comparison, variation was far higher in terms of $\delta^{13}\text{C}$. The scrapers *Acanthurus dussumieri*, *Acanthurus triostegus*, *Ctenochaetus striatus*, *Scarus frenatus* and *S. schegeli* all showed high within region variability in $\delta^{13}\text{C}$. Similarly, the browsing species *Naso unicornis* (Acantharidae), *Kyphosus* spp. (Kyphosidae) and *Siganus argenteus* (Siganidae) showed high variability within regions for $\delta^{13}\text{C}$, with *Kyphosus* spp. exhibiting particularly high variance (6.67).

Mixing model outputs showed that the contributions of the different potential dietary sources varied considerably among regions in the reef-flat habitat for a range of consumer species. Based on MixSIR outputs, the brown alga *Lobophora variegata* (pooled with either *Turbinaria ornata* or *Dictyota* sp.) contributed the most to the diets of *Turbo* sp. at Mandu and Maud, whereas crustose coralline algae made the greatest dietary contributions to this gastropod species at Bundegi (Figure 5.3). A range of other potential sources also contributed to the diet of this species and the proportional contribution of those sources varied among regions. In comparison, *Lobophora variegata* pooled with *T. ornata*, and to a lesser extent EAM, contributed the most to the diets of *Tectus pyramis* at Mandu, but the main dietary sources differed for this gastropod species in the other two regions (Figure 5.3). For the urchin *Echinometra mathaei*, *L. variegata* (on its own or pooled with *T. ornata*), as well as EAM made the greatest contributions to its diets at both regions it was collected (Mandu and Maud).

Despite scarids being categorised as scrapers (Table 5.1), they showed high variability in their dietary sources (including macroalgae) among species and even within species (across regions). For *Chlorurus sordidus*, EAM was an important dietary source at Bundegi, while *Lobophora variegata* (pooled with *T. ornata* or *Dictyota* sp.) also contributed to its diet at

Mandu and Maud (Figure 5.4). Similarly, EAM was an important dietary source for *Scarus schegeli* at Bundegi, but red algae also contributed to its diet in this region. In comparison, macroalgae contributed mainly to the diet of this species at the other two regions. EAM also contributed to the diet of *S. ghobban* at Mandu, but its contribution was negligible at the other two regions where its diet comprised a mixture of macroalgae. In comparison, *S. frenatus* exhibited a mixture of dietary sources at Mandu and Maud, the two regions in which it was collected. There was considerable variability in the dietary sources across regions and within regions for each of these three scraper species (Figure 5.4).

The scrapers in Acantharidae, *Acanthurus dussumieri*, *Acanthurus triostegus* and *Ctenochaetus striatus*, showed similar high variability in their dietary sources across regions, as well as among species within a region. For example, the mixing models for *A. dussumieri* and *A. triostegus* identified high contributions of the foliose red alga *Hypnea pannosa* at Maud, and either *P. hornemanii* or *A. spicifera* at Bundegi, but foliose red algae made only small contributions to the diets of these species at Mandu where the diet was shown to be mixed (Figure 5.5). It should be noted that the contributions of these algal species to the diets were highly variable for each species and region, particularly at Bundegi. *Ctenochaetus striatus* was the only acanthurid species to show high contributions of EAM, and this was restricted to Bundegi.

In the case of browsers, both *Naso unicornis* and *Kyphosus* spp. almost exclusively assimilated nutrients from *Lobophora variegata* (pooled with *T. ornata* or *Dictyota* sp.) at Bundegi and Mandu (Figure 5.5). The latter species also ingested *T. ornata* to some degree (median = 0.25) at Maud. The foliose red alga *A. spicifera* made greater but variable contributions to both *N. unicornis* and *Kyphosus* spp in this region. In comparison, the diet of *Z. scopas*, another browsing species in Acanthuridae, consisted predominantly of foliose red algae (either *H. pannosa* or *A. spicifera*) within both regions it was caught, although their contributions were variable and the brown algae *L. variegata* and *Dictyota* sp. could also make high contributions at Maud. For browsers in Siganidae, namely *S. argenteus* and *S. doliatus*, the foliose red algae (either *H. pannosa* or *A. spicifera*) made high dietary contributions at Bundegi and Maud, but both EAM and the brown alga *Sargassum oligocystum* made relatively high contributions to the former species at Mandu (Figure 5.4).

Species and habitat comparisons

Similar to regional comparisons, macroalgae displayed relatively low variance components for $\delta^{15}\text{N}$ in habitat comparisons at Mandu (Table 5.3). In proportionate terms, the brown alga *Lobophora variagata* as well as articulated coralline algae and *Portiera hornemanii* exhibited high variability in $\delta^{15}\text{N}$ across habitats (Table 4.3, Figure 5.6). Variance components were generally higher for $\delta^{13}\text{C}$ than $\delta^{15}\text{N}$ for these algae (Table 5.3). Crustose coralline algae showed greatest variation within habitats for $\delta^{13}\text{C}$, while articulated coralline algae varied mainly across habitats (Table 5.3, Figure 5.6). In the case of EAM, variability was higher in $\delta^{13}\text{C}$, and this occurred within habitat.

The variance components of $\delta^{13}\text{C}$ were far higher than those of $\delta^{15}\text{N}$ for the invertebrates and fishes (Table 5.3). Variability in $\delta^{13}\text{C}$ was explained mainly by habitat differences for *T. pyramis*, *Turbo* sp. and *E. mathaei*, and for the scrapers *A. dussumieri*, *A. triostegus* and *C. striatus* (Table 5.3, Figure 5.6). In comparison, another scraper, *Scarus frenatus*, showed greater variability within habitats, which was similar to the browsing species *N. unicornis* and *Kyphosus* spp. (Table 5.3, Figure 5.6). Indeed, the variance of 13.19 for *Kyphosus* spp. within habitat was exceptionally high.

Similar to regional comparisons, the contributions of the different potential dietary sources varied considerably among habitats for consumer species at Mandu as shown by mixing model outputs. EAM and the brown alga *Lobophora variegata* made relatively high contributions (median >0.4) to the diet of the urchin *E. mathaei* at both lagoon and reef-flat habitats (Figure 5.7), although the range of contributions was high (5 percentile <0.2, 95 percentile >0.7). In contrast, a mixture of all sources contributed to the diet of this species in

the outer-reef habitat. EAM and *L. variegata* made similarly high contributions to gastropod *T. pyramis* in the lagoon habitat (median = 0.25 and 0.50 respectively), but their contributions varied widely in this habitat (Figure 5.7). EAM made lower contributions to the diet of this species in the reef flat habitat, while articulated coralline algae and the brown algae *Sargassum oliocystum* and *L. variegata* all made relatively high contributions in the outer-reef habitat. *Turbo* sp. exhibited similar dietary sources to *T. pyramis* in the outer-reef habitat, but its sources varied between this and the reef-flat habitat at Mandu (Figure 5.7).

In terms of nominally herbivorous fishes, a range of sources contributed to the diets of the scrapers, the including *S. ghabban* and *S. frenatus*, as well as the acanthurids, *Acanthurus blochii*, *Acanthurus dussumieri*, *Acanthurus triostegus* and *Ctenochaetus striatus* (Figures 5.7 and 5.8). Macroalgae made the greatest contributions to these scrapers, but the contributions of algal species varied among habitats and between fish species, and also varied within habitat and species. For example, the foliose red alga *P. hormenanii* made high contributions to *A. blochii* and *A. dussumieri* in the lagoon habitat (median >0.8), although its contributions were highly variable for the former species (Figure 5.8). In contrast, *S. oliocystum* made high contributions to the diet of *A. blochii* in the reef-flat habitat, albeit variable. For *A. dussumieri*, both *P. hormenanii* and *S. oliocystum* made high contributions in the reef-flat habitat, while *S. oliocystum* almost dominated its diet in the outer reef. Similarly, the sources to the diets of *A. triostegus* and *C. striatus* varied among habitats. EAM made relatively low contributions to the diets of most scrapers in all habitats (Figures 5.7 and 5.8).

For the browsers *N. unicornis* and *Kyphosus* spp., the brown alga *Lobophora variegata* dominated their diets in both reef-flat and outer-reef habitats (Figure 5.8). This alga made far lower, but more variable, contributions to the diet of *N. unicornis* in the lagoon habitat, while another brown alga, *S. oliocystum*, made far greater contributions to the diet of this browser in this habitat.

Table 5.1 – Nominally herbivorous fish species collected at Ningaloo Reef, with their designation to functional groups based on broad dietary data from the literature and web sources.

Species	Functional group	Diet	Reference
Acanthuridae			
<i>Acanthurus blochii</i>	Scraper	EAM	Cvitanovic et al. (2007)
<i>Acanthurus dussumieri</i>	Scraper	EAM	Cvitanovic et al. (2007)
<i>Acanthurus triostegus</i>	Scraper	EAM	Cvitanovic et al. (2007)
<i>Ctenochaetus striatus</i>	Scraper	EAM	Froese and Pauly (2011)
<i>Naso unicornis</i>	Browser	Large macroalgae	Choat et al. (2002); Hoey & Bellwood (2009)
<i>Zebrasoma scopas</i>	Browser	Thallate & filamentous algae	Choat et al. (2002)
Kyphosidae			
<i>Kyphosus bigibbus/cornelii</i>	Browser	Macroalgae	Clements and Choat (1997)
<i>Kyphosus vaigiensis</i>	Browser	Large macroalgae	Clements and Choat (1997); Choat et al. (2002)
Scaridae			
<i>Scarus frenatus</i>	Scraper	EAM	Bellwood and Choat (1990), Cvitanovic et al. (2007)
<i>Scarus ghobban</i>	Scraper	EAM	Cvitanovic et al. (2007)
<i>Chlorurus sordidus</i>	Scraper	EAM	Choat et al. (2002), Cvitanovic et al. (2007)
<i>Scarus schlegelii</i>	Scraper	EAM	Choat et al. (2002), Cvitanovic et al. (2007)
Siganidae			
<i>Siganus argenteus</i>	Browser	Macroalgae/filamentous algae	Paul et al. (1990)
<i>Siganus doliatus</i>	Browser	Macroalgae	Mantyka and Bellwood (2007a); Fox et al. (2009)

2011

Table 5.2. Results of two-way PERMANOVA for $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ for a range of primary sources and consumers collected across three regions (Bundegi, Mandu and Maud) in reef flat habitat at Ningaloo Reef Australia, including estimated variance component (and % variance). * = lack of homogeneity of dispersion.

Group/species	df	$\delta^{15}\text{N}$				$\delta^{13}\text{C}$			
		Region		Residual		Region		Residual	
		MS	P	Var (%)	df	MS	P	Var (%)	df
Phaeophyta									
Dictyota sp	1	0.51	0.055	0.112 (55.2)	6	0.09	0.091 (44.8)	0.000	6
Lobophora variegata	2	0.26	0.004	0.047 (62.9)	12	0.03	0.028 (37.1)	1.587 (67.8)	12
Sargassum oligocystum	2	3.14	0.000	0.209 (57.2)	40	0.16	0.156 (42.8)	0.362 (6.3)	40
Turbinaria ornata	1	3.72	0.002	0.960 (88.8)	6	0.12	0.121 (11.2)	0.629 (38.2)	6
Rhodophyta									
Crustose coralline algae	2	4.40	0.010	0.977 (63.0)	9	0.57	0.574 (37.0)	7.909 (74.9)	9
Articulated coralline algae	2	0.33	0.035	0.052 (40.9)	12	0.07	0.075 (59.1)	2.759 (79.8)	12
Acanthophora spicifera	1	0.04	0.241	0.003 (12.0)	8	0.02	0.024 (88.0)	3.058 (81.7)	8
Hypnea pannosa	1	0.31	0.005	0.066 (76.4)	7	0.02	0.020 (23.6)	0.019 (0.000)	7
Portia hornemanii	1	0.04	0.329	0.001 (1.5)	8	0.04	0.038 (98.5)	0.000	8
Magnoliophyta									
Halophila sp.	1	5.90	0.002	1.129 (81.8)	8	0.25	0.251 (18.2)	0.000	8
Cyanobacteria									
Cyanobacterial mat	1	15.45	0.001	2.997 (86.6)	8	0.46	0.463 (13.4)	0.278 (60.0)	8
Epilithic Algal Matrix									
EAM	2	0.37	0.641	0.000	14	0.72	0.720 (100.0)	0.000	14
Gastropoda									
Tectus pyramis	2	0.20	0.603	0.000	12	0.38	0.377 (100.0)	2.747 (90.7)	12
Turbo sp.	2	0.35	0.351	0.009 (2.7)	12	0.31	0.308 (97.3)	1.307 (47.7)	12
Echinodermata									
Echinometra mathaei	1	0.18	0.393	0.000	8	0.23	0.226 (100.0)	0.454 (39.0)	8
Acanthuridae									
Acanthurus dussumieri	2	0.78	0.006	0.193 (71.1)	8	0.08	0.078 (28.9)	0.734 (26.3)	8
Acanthurus triostegus	2	1.90	0.000	0.432 (85.7)	10	0.07	0.072 (14.3)	0.034 (13.9)	10
Ctenochaetus striatus	2	1.97	0.004	0.610 (81.7)	6	0.14	0.136 (18.3)	0.153 (33.1)	6
Naso unicornis	2	0.39	0.258	0.041 (14.0)	8	0.25	0.249 (86.0)	0.000	8
Zebrasoma scopas	2	0.74	0.134	0.116 (28.7)	9	0.29	0.289 (71.3)	0.013 (7.1)	9
Kyphosidae									
Kyphosus sp.	2	1.64	0.185	0.160 (15.9)	12	0.85	0.846 (84.1)	0.080 (1.2)	12
Scaridae									
Chlorurus sordidus	1	0.89	0.008	0.163 (69.1)	8	0.07	0.073 (30.9)	0.141 (31.8)	8
Scarus frenatus	1	0.00	0.931	0.000	6	0.06	0.059 (100.0)	0.191 (9.0)	6
Scarus ghobban	2	0.41	0.162	0.057 (23.1)	9	0.19	0.190 (76.9)	1.917 (57.9)	9
Scarus schlegelii	2	0.66	0.127	0.101 (28.5)	9	0.25	0.253 (71.5)	0.238 (8.9)	9
Siganidae									
Siganus argenteus	2	3.52	0.001	0.841 (79.0)	9	0.22	0.223 (21.0)	0.420 (16.4)	9
Siganus doliatus	1	0.48	0.126	0.088 (37.8)	6	0.15	0.145 (62.2)	0.000	6

Table 5.3. Results of two-way PERMANOVA for $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ for a range of primary sources and consumers collected across 3 habitats at Mandu, Ningaloo Reef Australia, including estimated variance component (and % variance). * = lack of homogeneity of dispersion.

Group/species	$\delta^{15}\text{N}$						$\delta^{13}\text{C}$					
	Habitat			Residual			Habitat			Residual		
	df	MS	P	Var (%)	df	MS	Var (%)	P	MS	df	MS	Var (%)
Phaeophyta												
<i>Lobophora variegata</i>	2	0.60	0.000	0.14 (94.1)	10	0.01	0.01 (5.9)	0.177	0.82	2	0.40	0.10 (80.2)
Rhodophyta												
<i>Crustose coralline algae</i>	2	3.00	0.019	0.48 (47.6)	6	0.54	0.54 (52.4)	0.706	1.14	2	3.27	3.27 (100.0)
<i>Articulated coralline algae</i>	1	0.15	0.011	0.03 (66.4)	0	0.01	0.01 (33.6)	0.007	11.15	1	0.87	0.87 (29.7)
<i>Portieria hornemanni</i>	1	0.37	0.002	0.07 (81.3)	8	0.02	0.02 (18.7)	0.530	0.23	1	0.52	0.52 (100.0)
Epilithic Algal Matrix												
EAM	2	0.41	0.601	0.00	14	0.78	0.78 (100.0)	0.528	5.59	2	8.37	8.37 (100.0)
Gastropoda												
<i>Tectus pyramis</i>	2	5.24	0.000	0.98 (74.6)	12	0.33	0.33 (25.4)	0.000	28.35	2	0.17	0.17 (29)
<i>Turbo</i> sp.	1	0.59	0.093	0.09 (35.1)	8	0.16	0.16 (64.9)	0.000	13.83	1	0.23	0.23 (7.8)
Echinodermata												
<i>Echinometra mathaei</i>	2	1.96	0.003	0.35 (64.2)	12	0.20	0.20 (35.8)	0.000	24.40	2	0.61	0.61 (11.3)
Acanthuridae												
<i>Acanthurus blochii</i>	1	0.37	0.290	0.02 (8.2)	6	0.28	0.28 (91.8)	0.392	2.00	1	2.22	2.22 (100.0)
<i>Acanthurus dussumieri</i>	2	2.40	0.002	0.56 (73.4)	9	0.20	0.20 (26.6)	0.000	20.70	2	0.89	0.89 (14.9)
<i>Acanthurus triostegus</i>	2	0.04	0.615	0.00	11	0.08	0.08 (100.0)	0.001	14.57	2	0.20	0.20 (6.2)
<i>Ctenochaetus striatus</i>	2	0.20	0.208	0.03 (26.5)	6	0.09	0.09 (73.5)	0.000	4.05	2	0.12	0.12 (8.1)
<i>Naso unicornis</i>	1	0.16	0.469	0.00	4	0.25	0.25 (100.0)	0.765	0.14	1	1.49	1.49 (100.0)
Kyphosidae												
<i>Kyphosus</i> sp.	2	1.60	0.451	0.00	9	1.86	1.86 (100.0)	0.175	27.33	2	13.19	13.19 (78.5)
Scaridae												
<i>Scarus frenatus</i>	1	0.13	0.264	0.01 (12.3)	6	0.08	0.08 (87.7)	0.594	1.39	6	4.39	4.39 (100.0)
<i>Scarus ghobban</i>	1	3.95	0.011	0.81 (71.2)	7	0.33	0.33 (28.8)	0.221	4.74	1	2.68	2.68 (85.3)

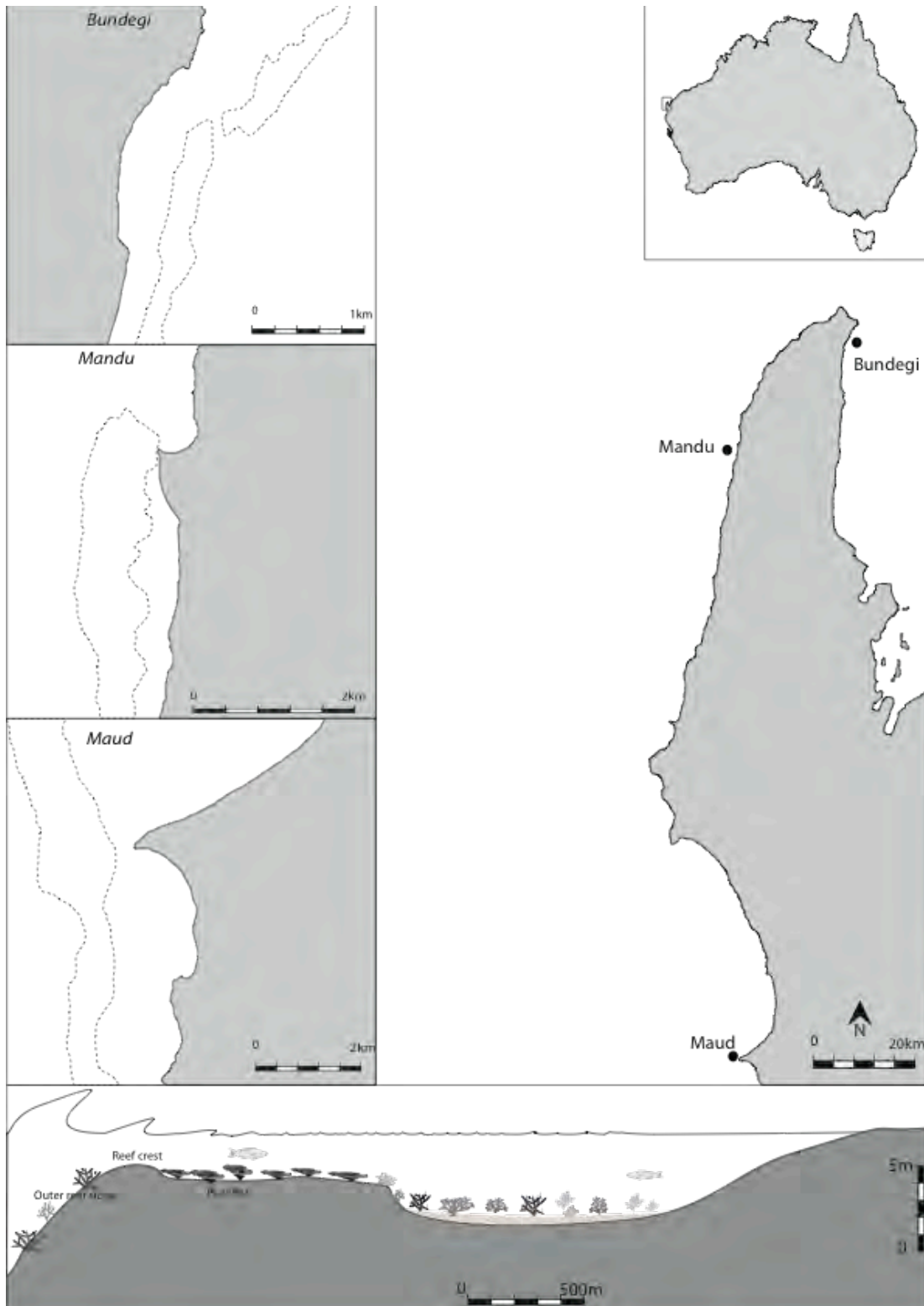


Figure 5.1. Map showing the location of regions sampled at Ningaloo Reef, west coast of Australia. Three inserts on the left show each of the three regions sampled, with the dotted lines indicating the boundaries of the reef flat. Bottom insert demonstrates the cross-section structure of the fringing reef environment, indicating the three habitats: reef slope, reef flat and lagoon.

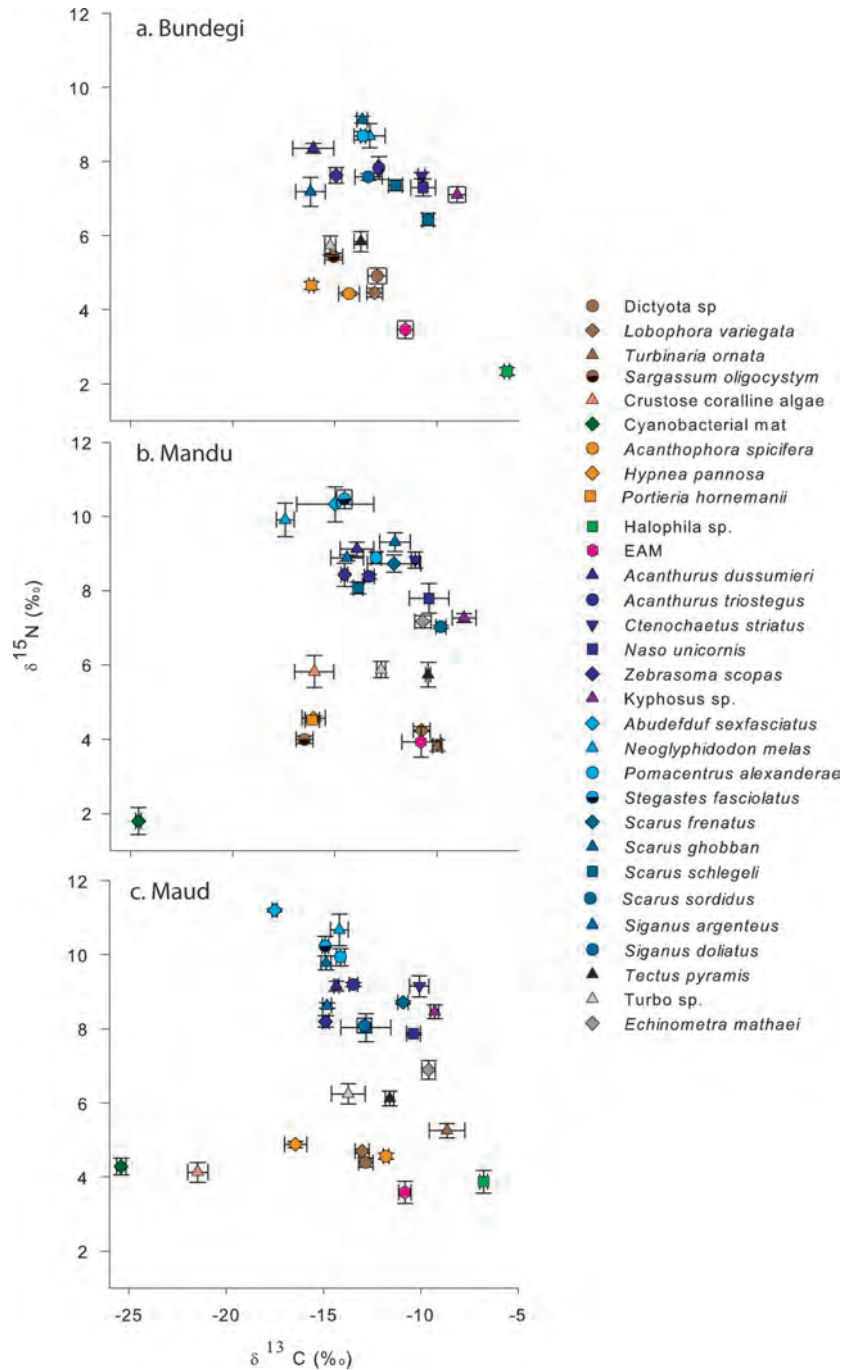


Figure 5.2. Mean $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values (\pm SE, $n=3-5$) for a range of primary sources and consumers collected in Reef Flat habitat across three regions (a. Bundegi, b. Mandu and c. Maud) at Ningaloo Reef, west coast of Australia.

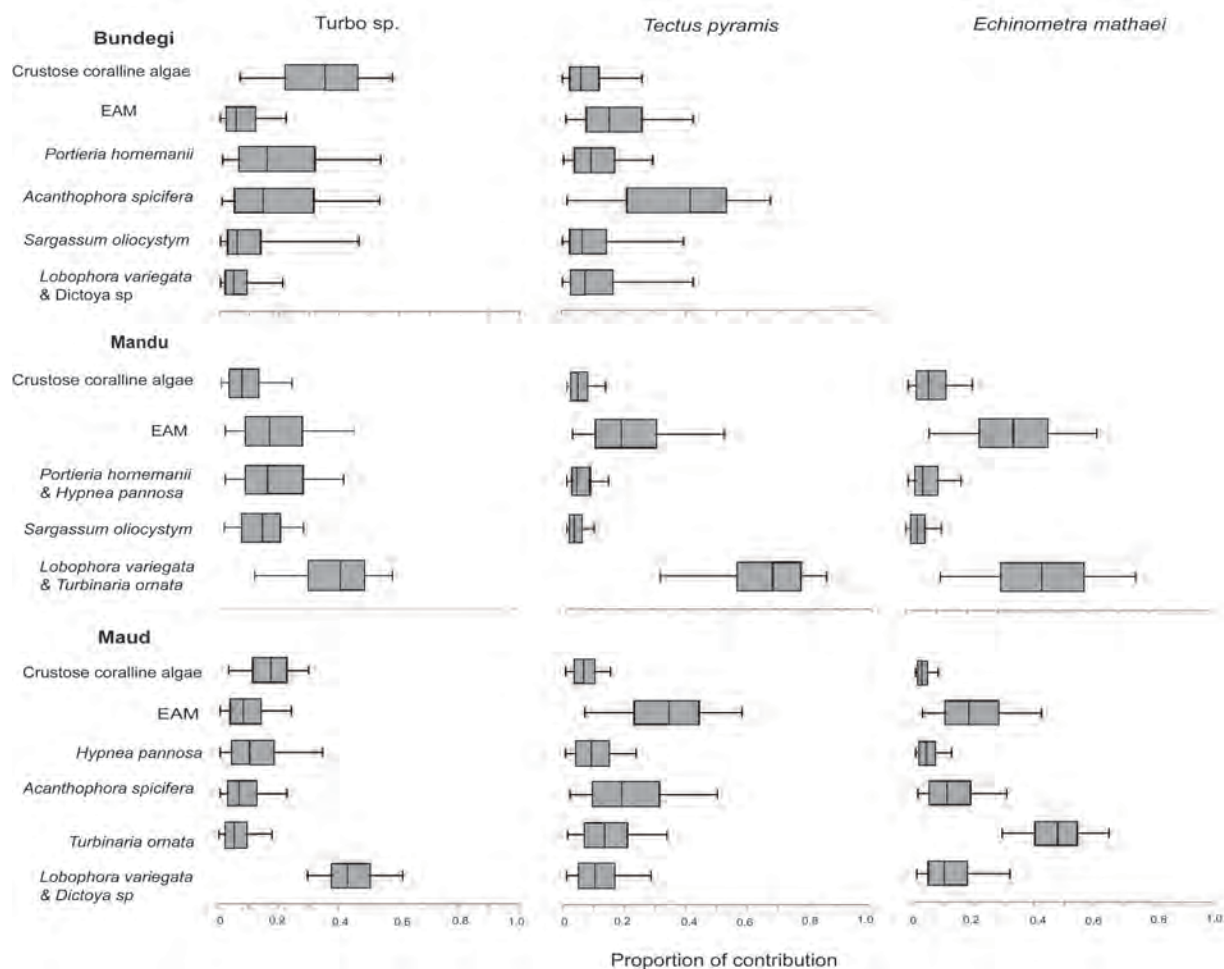


Figure 5.3. Mixing model outputs showing the proportional distribution of contributions of the main potential sources for the diets of three species of herbivorous invertebrates in the reef flat habitat in three regions of Ningaloo Reef, west coast of Australia. Lines indicate the 5 to 95 percentiles, grey bars indicate the 25 to 75 percentiles, and vertical line within shaded bar indicates the median value.

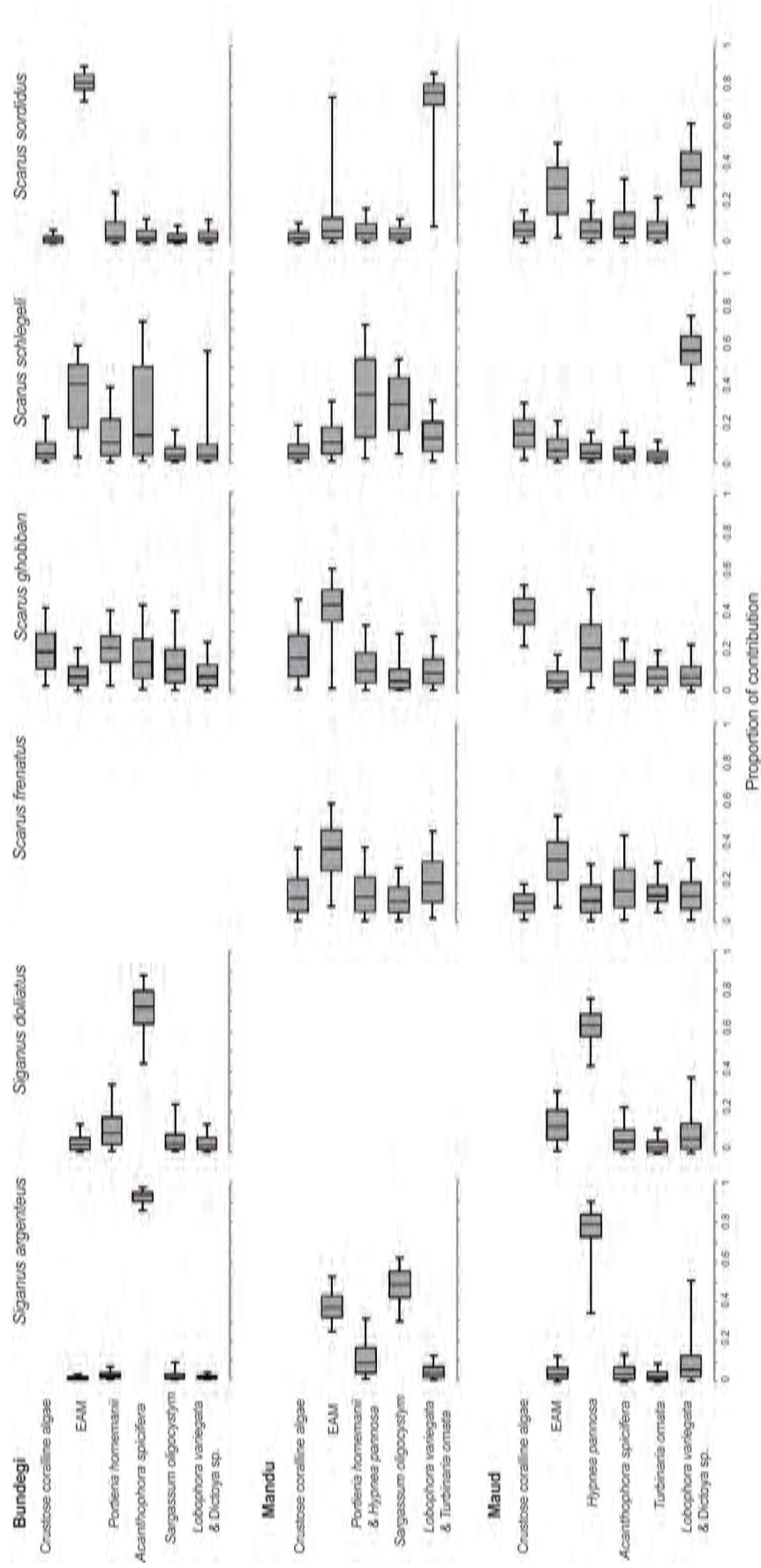


Figure 5.4. Mixing model outputs showing the proportional distribution of contributions of the main potential prey sources for the diets of three species of Siganidae and three species of in the reef flat habitat in three regions of Ningaloo Reef, west coast of Australia. Lines indicate the 5 to 95 percentiles, grey bars indicate the 25 to 75 percentiles, and vertical line within shaded bar indicates the median value.

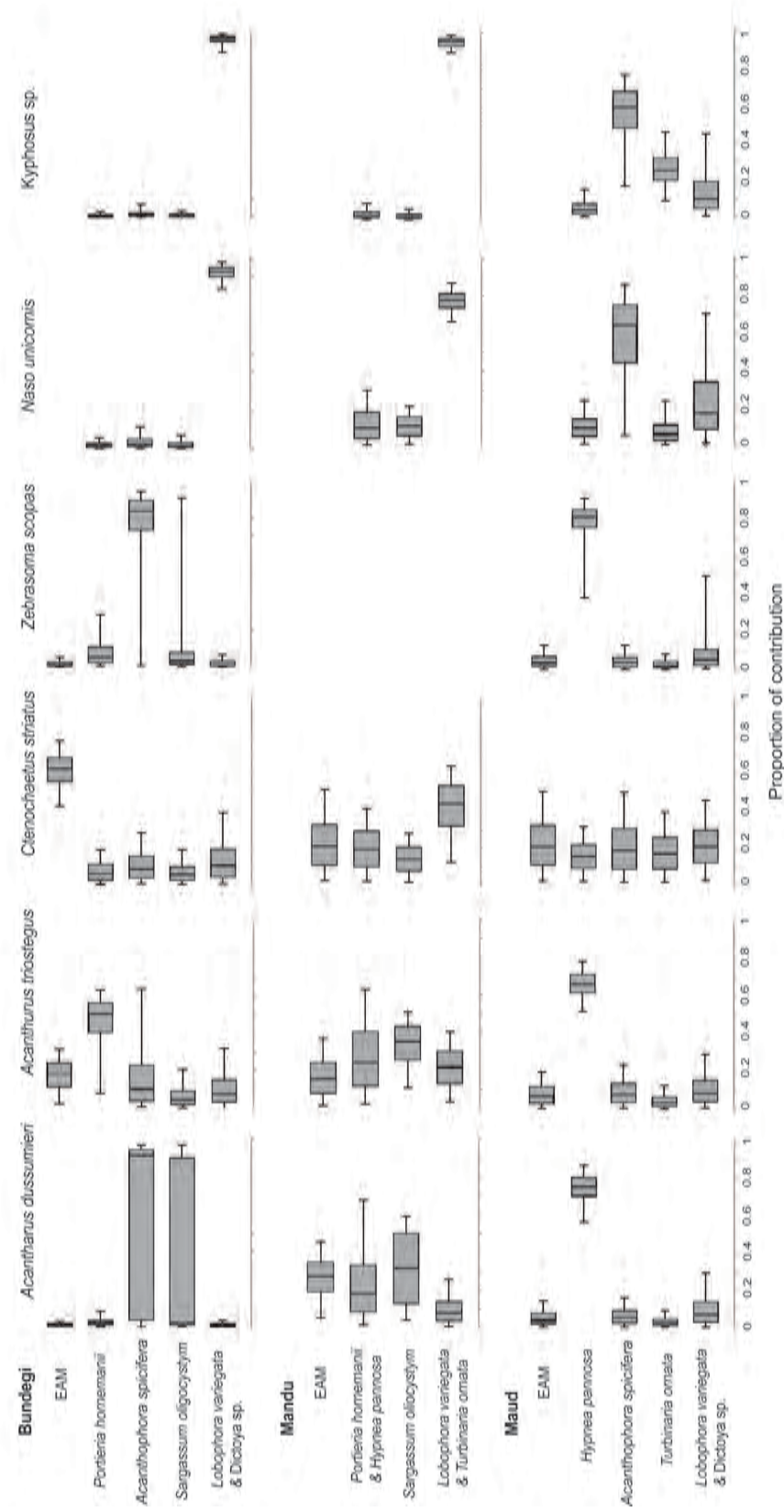


Figure 5.5. Mixing model outputs showing the proportional distribution of contributions of the main potential sources for the diets of five species of Acantharidae and Kyphosus spp. (Kyphosidae) in the reef flat habitat in three regions of Ningaloo Reef, west coast of Australia. Lines indicate the 5 to 95 percentiles, grey bars indicate the 25 to 75 percentiles, and vertical line within shaded bar indicates the median value.

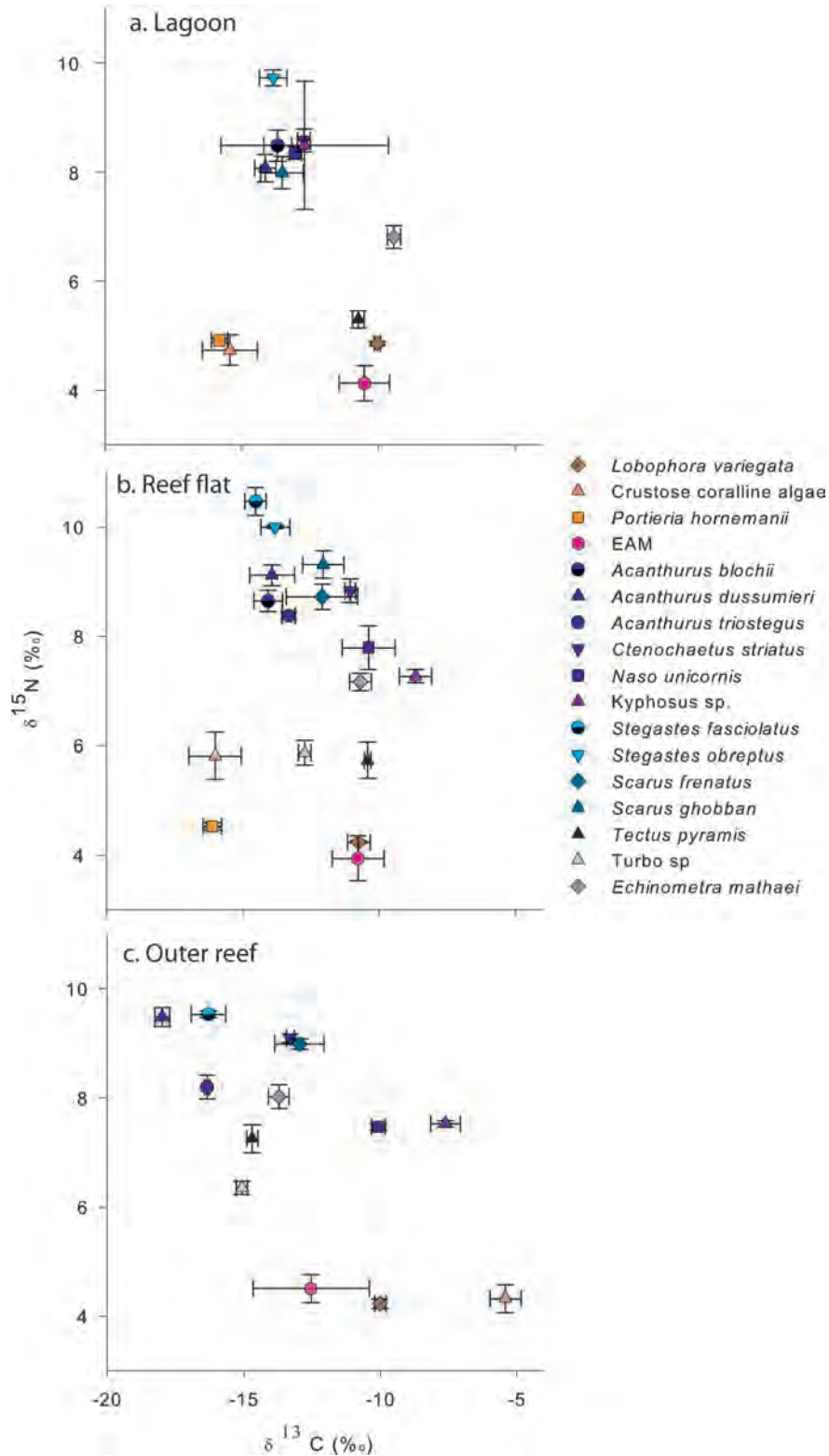


Figure 5.6. Mean $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values (\pm SE, $n=3-5$) for a range of primary sources and consumers collected across three habitats (a. Lagoon, b. Reef Flat and c. Outer Reef) at Mandu, Ningaloo Reef, west coast of Australia

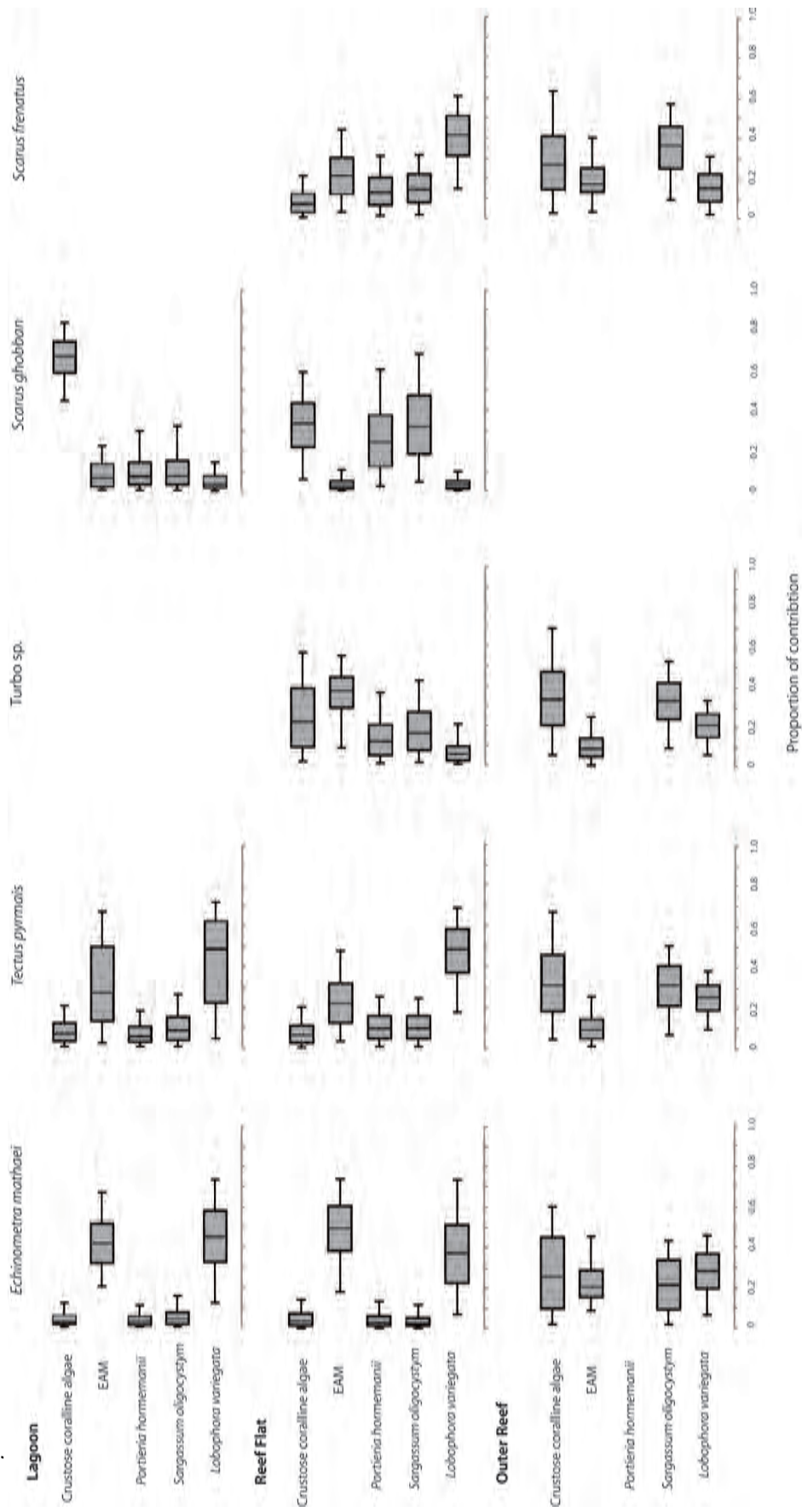


Figure 5.7. Mixing model outputs showing the proportional distribution of contributions of the main potential sources for the diets of three species of invertebrates and two species of Scaridae across three habitats at Mandu, Ningaloo Reef, west coast of Australia. Lines indicate the 5 to 95 percentiles, grey bars indicate the 25 to 75 percentiles, and vertical line within shaded bar indicates the median value.

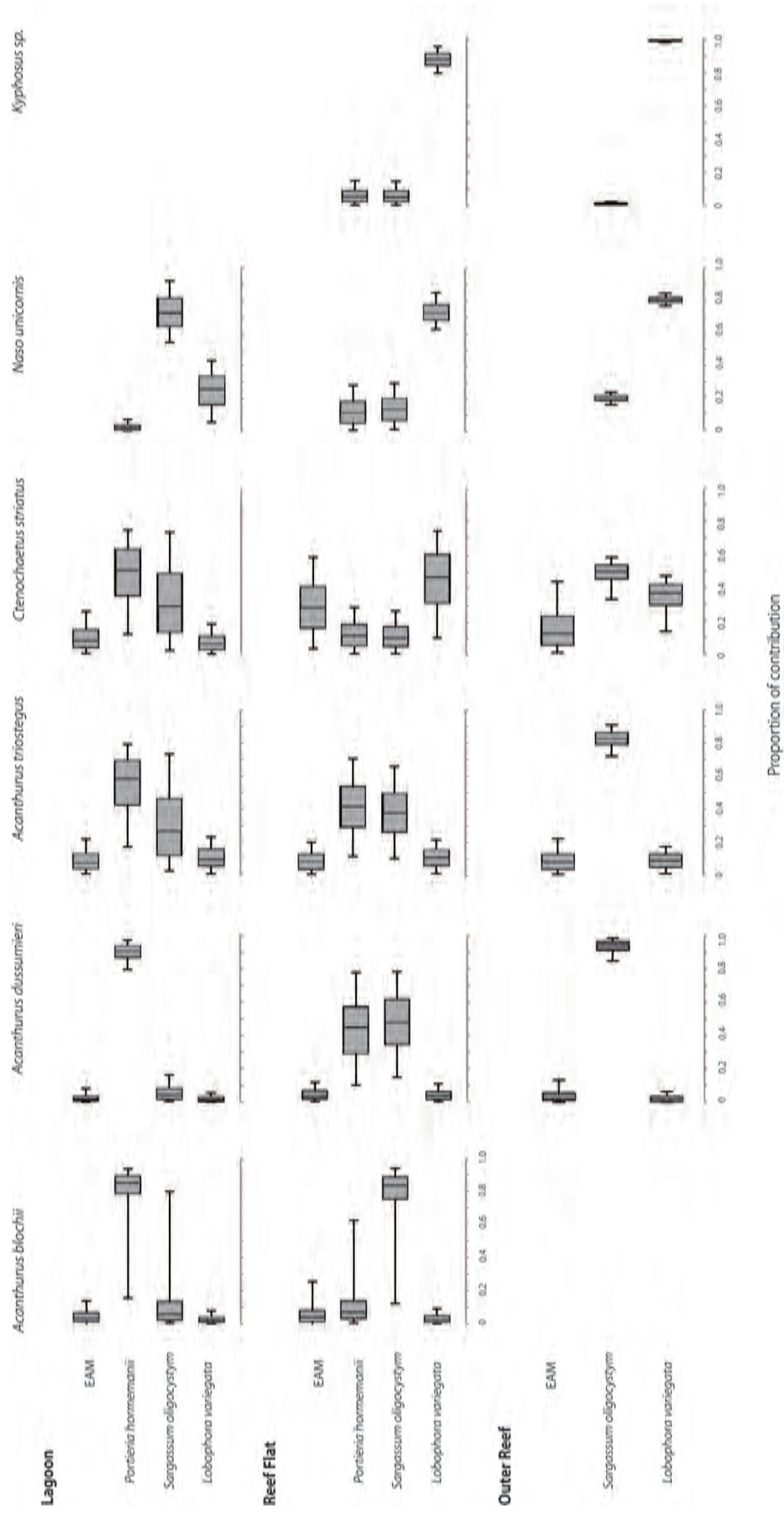


Figure 5.8. Mixing model outputs showing the proportional distribution of contributions of the main potential sources for the diets of four species of Acanthuridae and one species of Kyphosidae across three habitats at Mandu, Ningaloo Reef, west coast of Australia. Lines indicate the 5 to 95 percentiles, grey bars indicate the 25 to 75 percentiles, and vertical line within shaded bar indicates the median value.

Discussion

Variability among roving herbivores

Using stable isotopes ($\delta^{15}\text{N}$ and $\delta^{13}\text{C}$) and mixing models, our results suggest that macroalgae are common components in the diet of a wide range of roving herbivorous fish species in the coral-reef system at Ningaloo Reef on the eastern boundary of the Indian Ocean. This complements the results Chapters 2 and 3, which showed a high diversity of fish species biting assays of *Sargassum*.

The contribution of macroalgae to the diets of species designated as scrapers, including *S. schlegeli*, *S. ghobban*, *A. dussumieri*, *A. triostegus* and *C. striatus*, in this study is perhaps surprising given that these species are considered to consume EAM based on their jaw morphology, gut contents and fatty acids in their guts (Bellwood & Choat 1990, Choat et al. 2002, Choat et al. 2004). Scrapers are generally considered to play a negligible role in the removal of macroalgae (Hoey & Bellwood 2010b), but have exhibited high bite rates on *Sargassum* assays in the GBR and Ningaloo Reef (Fox & Bellwood 2007). At Ningaloo, *S. ghobban* and *S. schlegeli* were shown to contribute 10 and 29% of the bites on algal assays (Chapter 3), but they suggested that this may be associated with the ingestion of epiphytes on the macroalgae rather than the thalli itself. We cannot discount this, as we did not include epiphytes as a potential dietary source in our analyses and it is possible that they could exhibit similar stable isotope values to some of the macroalgae considered in our study. However, our observations indicate that epiphytes were not present in large quantities on the macroalgae collected during the study. Furthermore, *Scarus* species have been shown to consume a range of macroalgae, though they exhibit strong preferences for some over others (Mantyka & Bellwood 2007a). Thus, it is plausible that, while those scraper species often remove EAM, they may selectively ingest particular components of the EAM, e.g. microalgae. Alternatively, they may ingest macroalgae and therefore could play a greater role in the removal of macroalgae in coral-reef systems than previously thought.

Kyphosus vaigiensis and *N. unicornis* have been shown as major drivers of macroalgal herbivory in coral reefs in the GBR (Cvitanovic & Bellwood 2009, Hoey & Bellwood 2009, Bennett & Bellwood 2011) and at Ningaloo Reef (Chapters 3 and 4). Both species display high levels of macroalgal consumption, based on mass standardised bite rates of *Sargassum* assays, at both Ningaloo Reef (24.3% and 18.0%, respectively) and the Keppel Islands in the GBR (68.24% and 10.86%, respectively). The possession of gut flora that allows them to assimilate large algae allows them to feed on a range of macroalgae, including brown, red and green algae (Clements & Choat 1997).

The importance of the browsers *Naso unicornis* and kyphosids as grazers of macroalgae in coral-reef systems was further supported in the current study. *Naso unicornis* and *Kyphosus* spp. (*K. vaigiensis* and *K. biggus*) were shown to consistently assimilate large brown algae, including *Lobophora variegata* (with or without other brown algae), along with some foliose red algae. *Lobophora variegata* ranges in palatability across tropical regions, but appears to be palatable at Ningaloo Reef (see Chapter 2). In comparison, it was surprising that *Sargassum* was not shown to contribute substantially to their diet, since grazing rates by *Kyphosus* spp. on this brown alga can be high (Chapters 3 and 4). Also, feeding preference experiments indicated that *Sargassum* was consumed far more rapidly than *Lobophora* (Vergés, unpubl. data). The reef-flat habitat at Maud and Mandu is dominated by *Sargassum*, *Hypnea*, *Turbinaria* and *Lobophora* (Vanderklift, unpubl. data). While *Sargassum* is far more dominant in the lagoon habitat (Vergés, unpubl. data), few herbivorous species appear to occur in the reef-flat habitat (Chapter 3). However, this is likely to explain the high contribution of *Sargassum* to the diet of *N. unicornis* in the lagoon since it was shown to occur in this habitat. The limited contribution of *Sargassum* to the diets of those browsers in the reef-flat and reef-crest habitats in this study is likely to be due to the low availability of *Sargassum* and higher fish abundances in those habitats compared to the lagoon, suggesting a more finite food resource which could lead to other less palatable

algae, such as *Lobophora* and *Turbinaria* (Bolser & Hay 1996, Bittick et al. 2010) being consumed.

Compared to *N. unicornis* and kyphosids, our results suggest that other browser species, such as the siganids *S. argenteus* and *S. doliatus* and the acanthurid *Z. scopas* appeared to rely less on large brown macroalgae and more on foliose red algae or EAM at Ningaloo. Despite *Siganus* species being responsible for large numbers of bites on *Sargassum* assays in both Ningaloo Reef and Keppel Islands in the GBR, they contribute little to the removal of this macroalga only in the former region (Vergés et al. Chapter 3, Micheal et al. Chapter 4, Bennett & Bellwood 2011). Similarly, while *Z. scopas* was shown to take large numbers of bites of *Sargassum* assays, it was responsible for only small amounts of macroalgal removal at Ningaloo (Vergés et al. Chapter 3, Michael et al. Chapter 4). This is perhaps not surprising, given that the mixing models showed that all three species consumed a variety of algal sources at Ningaloo. Indeed, *S. doliatus* displays a greater preference for *Hypnea* (Mantyka & Bellwood 2007a) and perhaps other foliose red algae over brown algae. The long-term assimilation of material from a range of sources shown through the present study suggests that large brown macroalgae are not the main dietary source for these species.

Invertebrates consumed a range of macroalgae particularly, with evidence of some EAM also being consumed. Some degree of consistency was evident across species, particularly at Mandu where *Lobophora/Turbinaria* and EAM formed the main part of the diets of both species of gastropod and the urchin. *Turbo* spp. feed on a range of macroalgae (Trowbridge 1995, Foster et al. 1999, Wernberg et al. 2008), but some species prefer large brown algae (Cox & Murray 2006). Similarly, urchins, including *Echimometra* species, feed on a range of algae, including red and brown algae (de Loma et al. 2002, Yatsuya & Nakahara 2004). Despite *Turbinaria* being considered to be unpalatable (Bittick et al. 2010), it forms a major part of the diet of the urchin *Tripneustes gratilla* in a French Polynesian coral-reef system (de Loma et al. 2002). This species has also been shown to ingest detritus (de Loma et al. 2002). Thus, the consumption of *Lobophora* and *Turbinaria*, possibly as early recruits, as well as EAM, by *E. mathaei* is highly plausible.

Spatial variability in the importance of food sources to herbivores

Naso unicornis and *Kyphosus* spp., which are the main browsers at Ningaloo Reef (Vergés et al. Chapter 3, Michael et al. Chapter 4), almost consistently consumed brown algae across habitats and regions separated by 100s of metres and 10s of kilometres, respectively. The predicted contributions of brown algae to *N. unicornis* and *Kyphosus* spp. were highly uniform across regions or habitats, with 5-95 percentiles being similar to the medians for those sources at Bundegi and Mandu, and in the outer reef, reef flat and lagoon for the latter region. Furthermore, the variance components of particularly $\delta^{13}\text{C}$ for both fish species were greater at the within-region or within-habitat level, which could partly reflect similar patterns in the variance components for all brown algae. Thus, stable isotopes of sources and consumers varied at the level of individuals rather than at broad spatial levels.

Foliose red algae made greater contributions to the diets of a range of browsing species, including *N. unicornis* and *Kyphosus* spp. at Maud where *Acanthophora spicifera* made higher contributions to their diets. This does not appear to be related to shifts in food availability since algal assemblages are similar between Maud and Mandu (Vanderklift, unpubl. data), but may partly reflect the higher variability in the stable isotope values across regions for this red alga. In comparison, the contributions of foliose red algae to the diet of the rabbitfish *Siganus doliatus* were more consistent across regions, consuming either *Hypnea* or *A. spicifera*. Since this fish species has been shown to strongly select *Hypnea* on the GBR (Mantyka & Bellwood 2007a), consistency in its diet is likely to reflect food preferences. In comparison, the diet of *S. argenteus* was more variable across regions, suggesting that this species exhibits lower levels of selection of its food sources like *S. canaliculatus* on the GBR (Mantyka & Bellwood 2007a). Assimilated food for *S. argenteus* may thus reflect changes in access to its preferred food resources.

Even species that are considered to graze on EAM showed high variability in their food sources among regions and habitats, though there was also high variation within region and habitat. For example, the diet of *S. sordidus* was dominated by EAM at Bundegi, but by brown algae at Mandu. Since EAM was also a major component of the diet of *S. schlegeli* at Bundegi but not Mandu, the dominant food sources may reflect EAM availability.

Invertebrates also generally showed a high degree of variability in stable isotopes among habitats but not regions, and their food sources varied among regions. Diets of *Echinometra* spp. and other urchins have been shown to reflect the abundance of algae and thus availability (Cobb & Lawrence 2005, Hiratsuka & Uehara 2007), suggesting that the variability across regions and habitats likely reflects the availability of, or access to, food resources. As stated earlier, *Echinometra* spp. have been shown to consume *Turbinaria ornata* or other brown algae, suggesting that access to these resources may determine the type of food assimilated by these grazers.

CHAPTER 6. The role of herbivory on the spatial distribution of recruiting and established algal communities in coral versus algal dominated habitats

Christopher Doropoulos, Adriana Vergés, David Abecasis, Glenn A. Hyndes

Introduction

The replacement of corals by fleshy macroalgae is a common effect of large scale reef degradation on coral reefs due to disturbance, nutrient loading, and reduced trophic function (Hughes 1994, Bellwood et al. 2004, Sandin et al. 2008). The shift from coral to macroalgal dominance on coral reefs can occur as a result of disturbance and mortality to the coral community (Done 1992, Hughes 1994), after which algae can proliferate due to their competitive advantage in recruitment, rapid growth, and early dominance of newly available space (Littler & Littler 1999, Diaz-Pulido & McCook 2002, Connell et al. 2004). Interactions between coral and algae affect the benthic community structure on coral reefs, and are influenced by direct coral-algal competition (Jompa & McCook 2002, Diaz-Pulido et al. 2009) and indirectly by herbivory (Sammarco 1980, Lirman 2001, Hughes et al. 2007). The lack of a diverse herbivore community reduces the resilience of reefs and their ability to recover following disturbances, which can result in a phase-shift from coral to macroalgal dominated ecosystems (Hughes 1994, Scheffer et al. 2001, Bellwood et al. 2004, Cheal et al. 2010).

The dramatic phase-shifts from coral to algal dominance observed in some coral reefs has resulted in the widespread perception of abundant macroalgae as characteristic of degraded coral reef ecosystems. Two main processes are often proposed to greatly influence macroalgal abundance in degraded systems: anthropogenic nutrient loading (bottom-up effects) and overharvesting of herbivore populations (top-down effects) (Burkepile & Hay 2006). In coral reefs, many studies have investigated the relative importance of these two processes (e.g. Hatcher & Larkum 1983, Lapointe 1997, Smith et al. 2001, Diaz-Pulido & McCook 2003, McClanahan et al. 2003, Albert et al. 2008, Smith et al. 2010), and a recent meta-analysis of 54 field experiments revealed that herbivores have a greater effect on algal production and distribution compared to nutrient inputs (Burkepile & Hay 2006). Herbivores can directly influence algal abundance by consuming both the algal recruits (Diaz-Pulido & McCook 2003) and adults (Hoey & Bellwood 2010b, Bennett & Bellwood 2011). They often suppress the growth of turf and upright macroalgae, and their removal can cause algal proliferation leading to reduced juvenile and adult coral abundance and growth (Sammarco 1980, Lirman 2001, Jompa & McCook 2002, Box & Mumby 2007, Hughes et al. 2007, Birrell et al. 2008). Although grazers are a significant component of reef resilience by mediating coral-algal competition, few studies have examined the effect of herbivory on both recruiting and adult algal community dynamics.

Coral reefs are complex ecosystems that are characterised by spatial mosaics of different habitats. Recent studies have challenged the traditional view that intact reefs are only coral dominated habitats with small algal populations and propose that relatively healthy coral reef ecosystems may be regarded as spatial mosaics of adjacent coral- and algal-dominated benthic communities (Wismer et al. 2009, Johansson et al. 2010, Vroom & Braun 2010). Macroalgal abundance is often related to space availability and coral cover (McCook et al. 2001, Williams et al. 2001). Algal recruitment experiments demonstrate that high levels of herbivory can significantly decrease the amount of fleshy algae recruiting to new substrates (Diaz-Pulido & McCook 2003, McClanahan et al. 2003, Burkepile & Hay 2006), which is often correlated with increased levels of bare substrata and crustose coralline algae (CCA) (Hixon & Brostoff 1996, McClanahan 1997, Belliveau & Paul 2002, Albert et al. 2008). Yet, there is often high spatial and temporal variability associated with algal recruitment and herbivory in reef ecosystems (Airoldi 2000, Williams et al. 2001, Paddock et al. 2006, Bonaldo & Bellwood 2011). Indeed, local processes can affect the distribution of both benthic algae and herbivores, which creates patchiness in reefs (Klumpp & McKinnon 1992, Hixon &

Brostoff 1996, Airolidi 2000). Thus, herbivory is likely to play a different role on algal recruitment dynamics in adjacent reef habitats by influencing both the recruiting and adult algal communities.

In this study, we aimed to determine the effect of herbivory and habitat type on the algal community dynamics of a relatively pristine coral reef ecosystem, Ningaloo Reef (Western Australia). Monitoring surveys were conducted for nine months to identify seasonal patterns of the benthic and herbivorous fish communities in lagoon and reef-flat habitats: two distinct neighbouring areas of coral reefs dominated by algae and coral, respectively, in terms of percentage cover of substratum (Vergés *et al.* Chapter 2). A manipulative experiment was set up to quantify the effects of habitat and herbivory on algal recruitment over a six month period, using recruitment tiles and herbivore exclusion cages. We tested the hypotheses that: (1) algal recruitment would differ between the two habitats; and (2) this would be influenced by herbivory.

Materials and Methods

Study location

This study was conducted in the Ningaloo Marine Park, Western Australia, a coral reef with high levels of endemism and diversity (Roberts *et al.* 2002) that has been managed as a marine park since 1987, and was rezoned in 2005 to include 33% of the park as sanctuary (CALM & MPRA 2005). It is found in an arid-zone system that is not subject to any major anthropogenic threats and is generally considered pristine (Johansson *et al.* 2010). Ningaloo Reef is the largest fringing reef in Australia and the only extensive fringing reef on the west coast of any continent (Collins *et al.* 2003). It is a narrow fringing reef approximately 270 km in length that forms a discontinuous barrier adjacent to the North-west Cape, between the latitudes 21° 47' E and 24° 00' S. It consists of 16 major habitat types, differing in relative dominance of coral, macroalgal, and sand/rubble cover depending on the habitat type within this large coral reef ecosystem (Cassata & Collins 2008). The outer reef slope and crest are exposed to high wave energy that forms typical spur and groove morphology to depths of 30 m and support a diverse hard coral assemblage (Cassata & Collins 2008). The reef flat and lagoon are protected from this wave energy and are influenced by tidal movement which has a maximum range of ~2m during spring tides. The reef flat is dominated by tabulate *Acropora* and the lagoon is dominated by rubble, sand, and patches of fleshy macroalgae (Cassata & Collins 2008).

We conducted our study from August 2008 until May 2009 in the Mandu sanctuary zone (22° 08' S, 113° 45' E) towards the northern section of Ningaloo Reef. Mandu sanctuary is approximately 8 km long by 2 km wide, and has a lagoon ~600 m wide and a reef flat ~400 m wide. We haphazardly selected two sites within each lagoon and reef-flat habitat, with the lagoon and reef-flat sites separated by ~400 m, and each site within a habitat separated by ~400 m.

Fish community characterisation

Fish abundance and biomass were characterised for each site in three seasons: spring (November 2008), summer (February 2009) and autumn (May 2009). A diver swam a 25 m transect at a constant speed (ca 8 minutes per transect) and counted the abundance and size class (to 5 cm) of individual nominally herbivorous fish along 2.5 m on both sides of the transect line. Four replicate transects were conducted at each site at each time period, and each transect was separated by at least 10 m. Abundance data was converted to biomass using the allometric length-weight conversions $W = a * TL^b$, where W is weight in grams, TL is total length in cm, and parameters a and b are constants obtained from the literature (Froese & Pauly 2005). Fish surveys were always conducted at least two hours after sunrise and two hours before sunset. Individuals were recorded from the four major roving herbivore

families to the lowest possible taxa (generally to species, always to genus). We recorded a total of 20 species from the Acanthuridae, Kyphosidae, Labridae (parrotfish) and Siganidae families. Initial phase parrotfish were recorded as a single group (*Scarus* IP).

Benthic community characterisation

Macroalgal biomass was measured by clearing three 0.25 m² haphazardly placed quadrats of all macroalgae (thalli larger than 2 cm) at each site-habitat combination. Macroalgal biomass was sampled in the same three seasons described above for the fish assemblages. Algal samples were bagged and returned to the laboratory, where they were sorted to genus level (where possible) and weighed. Algal taxa that we were unable to identify were classified according to broad functional groups (brown, green or red; filamentous, encrusting or foliose).

To capture seasonal changes in the benthic community composition in each habitat, the benthos was surveyed at each site-habitat combination over a year. Surveys took place in winter (August 2008), spring (November 2008), summer (February 2009) and autumn (May 2009). Benthic communities at each site in the lagoon and reef-flat habitats were sampled using a line intercept method following Fox and Bellwood (2007). A 10 m transect tape was laid haphazardly across the reef, and a diver recorded the nature of the substrate directly touching the tape measure at 1 m interval points and at points 1 m perpendicular to the right and left of the tape. The substrate categories used were: live coral; CCA; epilithic algal matrix (EAM; *sensu* Wilson et al. (2003) which includes dead coral, turf algae, and detritus); fleshy macroalgae (> 1cm height); and sand. We conducted a total of 6 replicate transects at each site in the lagoon and reef-flat habitats (total of 30 points per replicate).

Algal recruitment experimental design

To assess the influence of large herbivorous fish on algal recruitment in habitats dominated by either macroalgae or coral, herbivore exclusion cages were installed at the two sites in the lagoon and reef flat. The cages were triangular in shape, and measured 50 x 50 x 50 cm. The corners were marked with rebar, to which PVC coated wire mesh (2.5 x 2.5 cm mesh size) was attached. In the caged plots, the wire material covered all sides and the top of the plots. A skirting edge on the sides of the cages was designed to prevent large benthic invertebrates from accessing the cages. Open (uncaged) plots were marked with the rebar, and partial cages were used as a control for cage artefacts and consisted of one side and a roof – to maintain the potential influence of the cage while allowing access to all herbivores. We installed six plots per treatment per site, and these were scrubbed clean once a month throughout the experimental period. Some of the plots at the reef-flat sites, from all three treatments, became inhabited by territorial damselfish. These fish were not removed but were included in analyses as a covariate due to their influence on benthic algal communities (see review by Ceccarelli et al. 2001).

Recruitment tiles were installed in the plots in August 2008 and collected in February 2009. The tiles measured 10 x 10 cm and were made from PVC. Although PVC is not a natural substrate, studies have demonstrated that algal community composition is not altered by this material compared to natural materials made from dead corals in long-term algal recruitment experiments (Hixon & Brostoff 1996). The tiles were sanded to roughen the surfaces, which created irregular depressions on the tiles to allow for algal attachment (Hixon & Brostoff 1996, Smith et al. 2001, Smith et al. 2010). The recruitment tiles were attached to a piece of horizontal wire mesh, which was elevated 10 cm from the benthos in each plot. This standardised the attachment substrate and avoided smothering of the tiles by sediment.

In February 2009, six months after deployment, the two tile replicates from each plot were carefully removed and placed in individual zip-lock bags *in situ*. After collection, the tiles were frozen until laboratory processing. In the laboratory, each tile was thawed and rinsed with seawater to remove any sediment, and any small invertebrates were removed with

forceps. To determine the percent cover of the algal community on the top surface of each tile, a point-intercept method was used by placing a transparent plastic sheet with a grid of 25 dots on top of each tile. Using a dissecting microscope, the algae or substrata present beneath each point were classified into one of the following categories: bare tile, CCA, encrusting fleshy algae (EFA), turf algae (red, green or brown), and fleshy macroalgae (which included erect macrophytes such as *Dictyota*, *Laurencia*, *Lobophora*, *Padina*, and *Sargassum*).

Following classification, the algae from the tile was scraped and oven dried at 60° C for ≥ 48 hours, after which the algae were weighed to 10^{-4} g. In order to estimate fleshy algae biomass, we added HCl acid (10%) to the vials to remove any carbonate associated with sand, coralline algae, and shell fragments. Vials were again placed in the oven at 60° C for ≥ 48 hours and reweighed.

Data analyses

Initial inspection of each univariate data set was conducted to check for normal distribution using the K-S test, and if the data did not conform to a normal distribution after transformation it was analysed using *P* values generated from 9999 permutations. Homogeneity of variance was explored using Cochran's test for univariate data and with permDISP for multivariate data. Bray-Curtis similarity was used to create resemblance matrices for all multivariate data, which were analysed with *P* values generated from 9999 permutations. When necessary, the data were transformed to meet the assumptions of homogeneity. When overall significant differences were found ($P < 0.05$), pair-wise comparisons were conducted.

Total herbivore and algal biomass were tested using mixed effects analysis of variance (ANOVA) with habitat (2 levels) and season (3 levels) as fixed factors and site (2 levels) included as a random factor nested in habitat. The biomass of the fish and algal communities were used to assess patterns in their composition using mixed effects multivariate analysis of variance (PERMANOVA) with the same model described above. To investigate benthic community cover we used the same mixed effects PERMANOVA model, but with 4 levels for season. We then analysed the percent cover of each benthic group using permutational ANOVA with the model described. Principal coordinate analysis (PCO) was conducted to visualise similarities between the fish, algal, and benthic communities amongst habitats using Bray-Curtis distance as our metric. We investigated the taxa that contributed most strongly to the dissimilarities from the different habitats by using correlations > 0.6 based on Spearman ranking.

The mean percent cover on the top surface of the tiles was used to analyse the composition of the recruiting algal community using a mixed effects multivariate analysis of covariance (PERMANCOVA). Habitat (2 levels) and herbivory (3 levels) were included as fixed factors, with site (2 levels) included as a random factor nested in habitat. Damselfish were included as the covariate because they established territories in some of the experimental plots in the reef-flat sites. Following this, the mean percent cover of each individual functional group and the total fleshy algal biomass were analysed using permutational ANCOVA with the same model.

All ANOVAs were performed using GMAV5 (coded by A. J. Underwood and M. G. Chapman, University of Sydney, Australia). Permutation, covariate, and multivariate analyses were performed using Primer-E v6 (Clarke & Gorley 2006) with the PERMANOVA+ add-on package (Anderson *et al.* 2008b).

Results

Roving herbivorous fish biomass and community composition

Significant differences in the total biomass of roving herbivorous fish were found between the lagoon and reef-flat habitats, where the biomass in the reef-flat was at least an order of magnitude higher than the lagoon (Table 6.1a; Fig. 6.1a). In contrast, we detected no significant differences in total herbivorous fish biomass between seasons or sites (Table 6.1a). The herbivorous fish community composition also differed significantly between the lagoon and reef-flat habitats, and there were no clear seasonal patterns in fish community composition (Table 6.1b). The PCO of the herbivorous fish community composition yielded two components that explained 58.1 % of the variance (Eigenvalues 31923 for PCO1 and 21084 for PCO2, Figure 6.2a). Although there was some overlap, the separation between the lagoon and reef-flat habitats were clustered predominantly on the PCO1 axis. Spearman ranking identified *Acanthurus triostegus*, *Chlorurus sordidus*, *Scarus rivulatus*, *S. schlegeli* and *Siganus argenteus* as the dominant species correlated with the reef flat, while *Acanthurus* sp. and *Scarus* IP were associated with both habitats. The samples from within both the lagoon and reef-flat habitats were spread across the PCO2 axis indicating variability in the herbivorous fish community across sites within habitats (Table 6.1b, Fig. 6.2a).

Benthic algal biomass and community composition

The total algal biomass was highly seasonal and it was greatest in the lagoon compared to the reef flat during autumn only (significant Habitat x Season interaction, Table 6.2a). Both reef habitats displayed a seasonal increase in algal biomass from spring and summer to autumn, but this was only significant in the lagoon where the change in fleshy algae biomass increased from ~40 to 187 g per 0.25m² (Fig 6.1b). In contrast, the benthic algal community composition displayed significant differences amongst the lagoon and reef-flat habitats, but this was not affected by seasonality (Table 6.2b). Although there was large site within habitat variability, there was some separation between the habitats on the PCO1 axis that explained 40.3 % of total variation (Eigenvalue 26189; Table 6.2b; Fig. 6.2b). The lagoon was characterised by *Sargassum*, whilst *Lobophora variegata* and *Hypnea* characterised the reef flat (Fig. 6.2b).

Benthic community cover

Multivariate analysis of the benthic community cover revealed a strong distinction between the lagoon and reef-flat habitats (Table 6.3). The community composition was separated on the PCO1 axis, which explained 89.4 % of the total variation (Eigenvalue 57638, Fig. 6.3). Spearman correlations indicated that differences between habitats were clearly driven by fleshy macroalgae and sand in the lagoon, and by live coral and EAM in the reef flat (Fig. 6.3). The lagoon had an average of ~27 % macroalgae cover (Fig. 6.4b), which was significantly higher than the reef flat in summer and autumn but not in winter and spring (significant Habitat x Season interaction, Table 6.4). The reef flat had an average of ~47 % live coral cover and ~27 % EAM cover (Fig. 6.4a and 6.4c), which were both significantly greater than in the lagoon (Table 6.4). Although CCA was generally higher in the reef flat compared to the lagoon (Fig. 6.4c), this was non-significant (Table 6.4).

Recruitment tile algal community composition and biomass

The community composition of the algae found on the recruitment tiles was strongly affected by the experimental herbivory treatments. Irrespective of habitat, algal community composition was significantly different between tiles excluded from herbivores (closed

treatments) compared to those exposed to herbivores (open and partial treatments; post-hoc analysis Closed \neq Partial = Open, Table 6.5). These differences were characterised by significantly higher cover of bare tile and fleshy macroalgae in the herbivore exclusion treatment, in both the lagoon and reef-flat habitats (Fig. 6.5a & 6.5e; Table 6.6). The presence of damselfish significantly affected the community composition of the algae present on the recruitment tiles (Table 6.5). Damselfish territories were only established at plots in the reef-flat sites, where their presence significantly increased turf cover compared to the lagoon habitat, irrespective of herbivore exclusion treatment (Fig. 6.5d; Table 6.6). Damselfish presence also tended to decrease CCA cover on the recruitment tiles in the reef-flat sites (Fig. 6.5c) but this effect only approached statistical significance ($p = 0.079$; Table S6). Within each habitat there was significant variability amongst sites in the multivariate analysis (Table 6.5) and for the CCA and turf cover in the univariate analyses (Table 6.6).

Following a similar pattern to the algal cover on the recruitment tiles, the biomass of fleshy algae was significantly higher on tiles from the herbivore exclusion treatments compared to those exposed to herbivores in both the lagoon and reef-flat habitats (Fig. 6.6; Table 6.7). Total algal biomass in the lagoon ($\sim 7 \text{ g } 100 \text{ cm}^{-2}$) was slightly higher than the reef flat ($\sim 4 \text{ g } 100 \text{ cm}^{-2}$), but this difference was not significant, probably due to the high variability between sites within each habitat (Table 6.7).

Table 6.1. Mixed effect (a) permutational ANOVA assessing total biomass and (b) PERMANOVA assessing community composition of herbivorous fish between habitats and seasons. Total biomass data were square root transformed and community composition was log ($x + 1$) transformed prior to analysis. Relevant significant probabilities are indicated in bold.

Source of variation	df	MS	Pseudo-F	P (perm)	Conclusion – Pair-wise
A. Total biomass					
Habitat	1	18528.0	130.18	0.0083	Lagoon < Reef flat
Season	2	2993.0	2.47	0.2000	
Site (Ha)	2	142.3	0.09	0.9431	
Ha x Se	2	2372.1	1.95	0.2578	
Se x Si (Ha)	4	1213.8	0.81	0.5944	
Residual	36	1496.6			
B. Community composition					
Habitat	1	20601.0	4.61	0.0269	Lagoon ≠ Reef flat
Season	2	1855.1	0.97	0.4759	
Site (Ha)	2	4459.2	3.38	0.0003	
Ha x Se	2	1456.0	0.76	0.6153	
Se x Si (Ha)	4	1907.1	1.45	0.109	
Residual	36	1318.1			

Table 6.2. Mixed effects (a) ANOVA assessing total biomass and (b) PERMANOVA assessing community composition of benthic algae between habitats and seasons. Community composition data were square root transformed prior to analysis. Relevant significant probabilities are indicated in bold. Pooling was in accordance with Underwood (1997).

Source variation	df	MS	F	P	Conclusion: SNK
A. <u>biomass</u>					
Habitat	1	39717.2	11.16	0.0025	Summer and Spring: Lag = RF; Autumn: Lag > RF Lagoon: Summer = Spring < Autumn; Reef flat: NS
Season	2	27061.0	13.32	0.0170	
Site (Ha)	2	4869.2	1.37	0.2722	
Ha x Se	2	17478.7	8.60	0.0356	
Se x Si (Ha)	4	2031.8	0.57	0.6860	
Pooled	26	3558.0			
Residual	24	3448.8			
B. <u>Community composition</u>					
Habitat	1	11825.0	4.89	0.0199	Lagoon ≠ Reef flat
Season	2	4258.6	2.45	0.1062	
Site (Ha)	2	2417.5	2.03	0.0366	
Ha x Se	2	2103.5	1.21	0.3427	
Se x Si (Ha)	4	1739.6	1.46	0.1081	
Residual	24	1192.4			

Table 6.3. Results of the mixed effects PERMANOVA assessing benthic community cover between habitats and seasons. Data were $\sin(\sqrt{x})$ transformed prior to analysis. Relevant significant probabilities are indicated in bold.

Source variation	df	MS	Pseudo-F	P (perm)	Conclusion: Pair-wise
Habitat	1	45734.0	85.38	0.0043	Lagoon ≠ Reef flat
Season	3	480.0	2.10	0.1001	
Site (Ha)	2	535.6	4.82	0.0054	
Ha x Se	3	673.0	2.94	0.0811	
Se x Si (Ha)	6	228.6	2.06	0.0507	
Residual	80	111.0			

Table S4. Results of the mixed effects permutational ANOVAs assessing live coral, crustose coralline algae (CCA), epilithic algal matrix (EAM), fleshy macroalgae, and sand cover between habitats and seasons. Data were $\sin^{-1}(x)$ transformed prior to analysis. Relevant significant probabilities are indicated in bold. Winter = Wi; Spring = Sp; Summer = Su; Autumn = Au.

Source of variation	df	Live coral			CCA			EAM			Fleshy macroalgae			Sand		
		Pseud o-F	P (perm)		Pseud o-F	P (perm)		Pseud o-F	P (perm)		Pseud o-F	P (perm)		Pseud o-F	P (perm)	
Habitat	1	293.97	0.0024		9.24	0.0956		180.02	0.0061		25.11	0.038		78.98	0.0126	
Season	3	0.31	0.8227		3.50	0.0954		4.18	0.0571		2.53	0.1585		3.80	0.078	
Site (Ha)	2	1.60	0.2031		1.18	0.3168		1.61	0.204		6.527	0.0024		4.26	0.0172	
Ha x Se	3	1.67	0.27		2.28	0.1829		1.33	0.3503		5.16	0.0405		1.51	0.3063	
Se x Si (Ha)	6	1.50	0.19		1.14	0.343		2.61	0.0228		2.67	0.0206		0.95	0.4777	
Residual	8															
	0															

Pair-wise tests for significant effects:

Live coral – Habitat: Lagoon < Reef flat
 EAM – Se x Si (Ha): Lagoon (1) Wi = Sp = Su > Au; Lagoon (2) Sp > Au, all other NS; Reef flat (1) Su > Wi = Au = Sp, Reef flat (2) all NS
 Macroalgae – Ha x Se: Season: Winter and Spring NS; Summer and Autumn Lagoon > Reef flat
 Habitat: Lagoon Summer < Autumn; all other NS; Reef flat Winter = Autumn > Summer, all other NS
 Sand – Habitat: Lagoon > Reef flat

Table 6.5. Results of the mixed effects PERMANCOVA assessing community cover on the recruitment tiles between habitats and herbivore exclusion. Damselfish presence/absence was included as a covariate. Data were $\sin(\sqrt{x})$ transformed prior to analysis. Pooling was in accordance with Underwood (1997). Relevant significant probabilities are indicated in bold.

Source of variation	df	MS	Pseudo-F	P (perm)	Conclusion: Pair-wise
Damselfish	1	17433.0	8.12	0.011	
Habitat	1	5141.1	2.59	0.313	
Herbivory	2	4262.9	4.17	0.044	Closed ≠ Partial = Open
Site (Ha)	2	3185.3	5.61	0.002	
Pooled	6	967.8			
Residual	59	543.5			

Table 6.6. Results of the mixed effects permutational ANOVAs assessing bare tile, encrusting fleshy algae (EFA), crustose coralline algae (CCA), turf algae, and fleshy macroalgae (MA) cover on the top side of recruitment tiles between habitats and herbivory. Damselfish presence/absence was included as a covariate. Data were $\sin^{-1}(x)$ transformed prior to analysis. Relevant significant probabilities are indicated in bold.

Source of variation	df	Bare tile			EFA			CCA			Turf			MA		
		Pseudo-F	P (perm)		Pseudo-F	P (perm)		Pseudo-F	P (perm)		Pseudo-F	P (perm)		Pseudo-F	P (perm)	
Damselfish	1	0.01	0.9184		2.77	0.136		4.18	0.0799		17.30	0.0011		1.60	0.2511	
Habitat	1	2.62	0.1798		0.01	0.9196		2.68	0.2245		2.31	0.2325		1.40	0.3046	
Herbivory	2	18.18	0.0116		1.03	0.4332		0.33	0.7482		2.83	0.1693		57.13	0.0031	
Site (Ha)	2	2.07	0.1357		1.28	0.2908		9.51	0.0004		5.82	0.0052		1.72	0.1908	
Da x He	2	0.84	0.4663		4.87	0.0383		0.50	0.6253		0.91	0.4484		1.82	0.2221	
Ha x He	2	0.03	0.9757		2.78	0.1638		0.07	0.9379		0.38	0.7136		0.77	0.5225	
He x Si (Ha)	4	0.51	0.7263		0.21	0.9269		4.39	0.004		1.29	0.2814		0.33	0.8513	
Da x He x Si (Ha)	1	1.49	0.2168		0.06	0.8212		1.85	0.1851		3.04	0.0872		0.04	0.8277	
Residual	56															

Pair-wise tests for significant effects:

Tile – Herbivory: C > O = P

EFA – Da x He: all NS

CCA – He x Si (Ha): Lagoon (1) C ≠ P = O; Lagoon (2) all NS; Reef flat (1) all NS; Reef flat (2) C = P, C ≠ O, P = O

MA – Herbivory: C > O = P

Table 6.7. Results of the mixed effect ANCOVA of fleshy algal biomass on the recruitment tiles between habitats and herbivore exclusion treatments. Damselfish presence/absence was included as a covariate. Data were log (x+1) transformed prior to analysis. Pooling was in accordance with Underwood (1997). Relevant significant probabilities are indicated in bold.

Source of variation	df	MS	Pseudo-F	P (perm)	Conclusion: pair-wise
Damselfish	1	1.52	1.94	0.2044	
Habitat	1	1.46	2.05	0.2723	
Herbivory	2	0.77	8.13	0.0005	Closed > Partial = Open
Site (Ha)	2	1.24	13.29	0.0001	
Pooled	65	0.09			

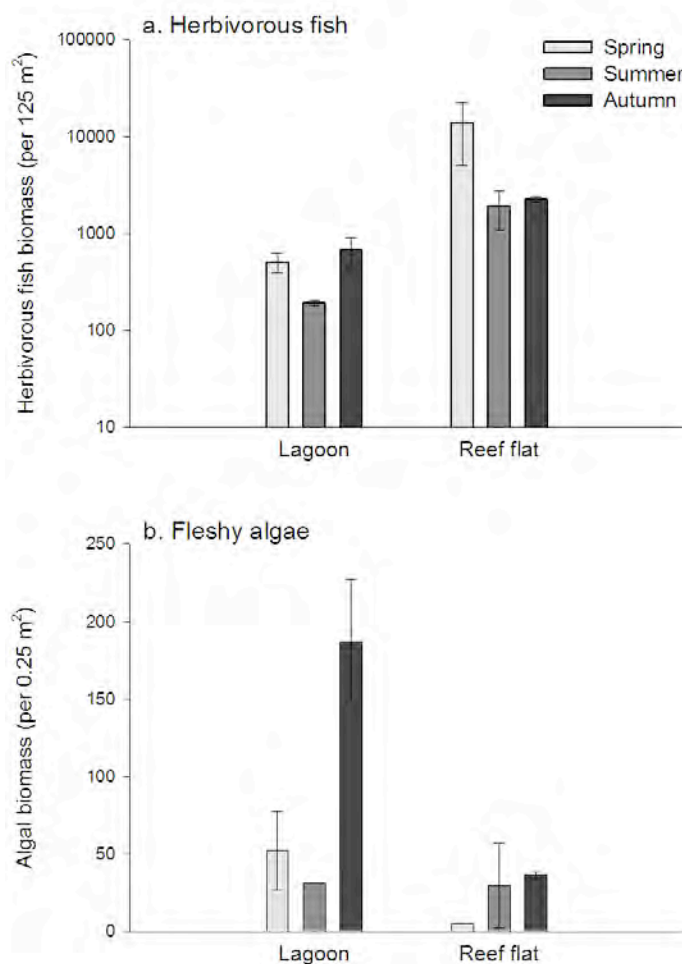


Figure 6.1. Mean biomass (\pm SE) of (a) herbivorous fish per 125 m² and (b) fleshy algae per 0.25 m² in the lagoon and reef-flat habitats during spring, summer and autumn, at Ningaloo Reef. Note the logarithmic scale on the y axis for herbivorous fish biomass.

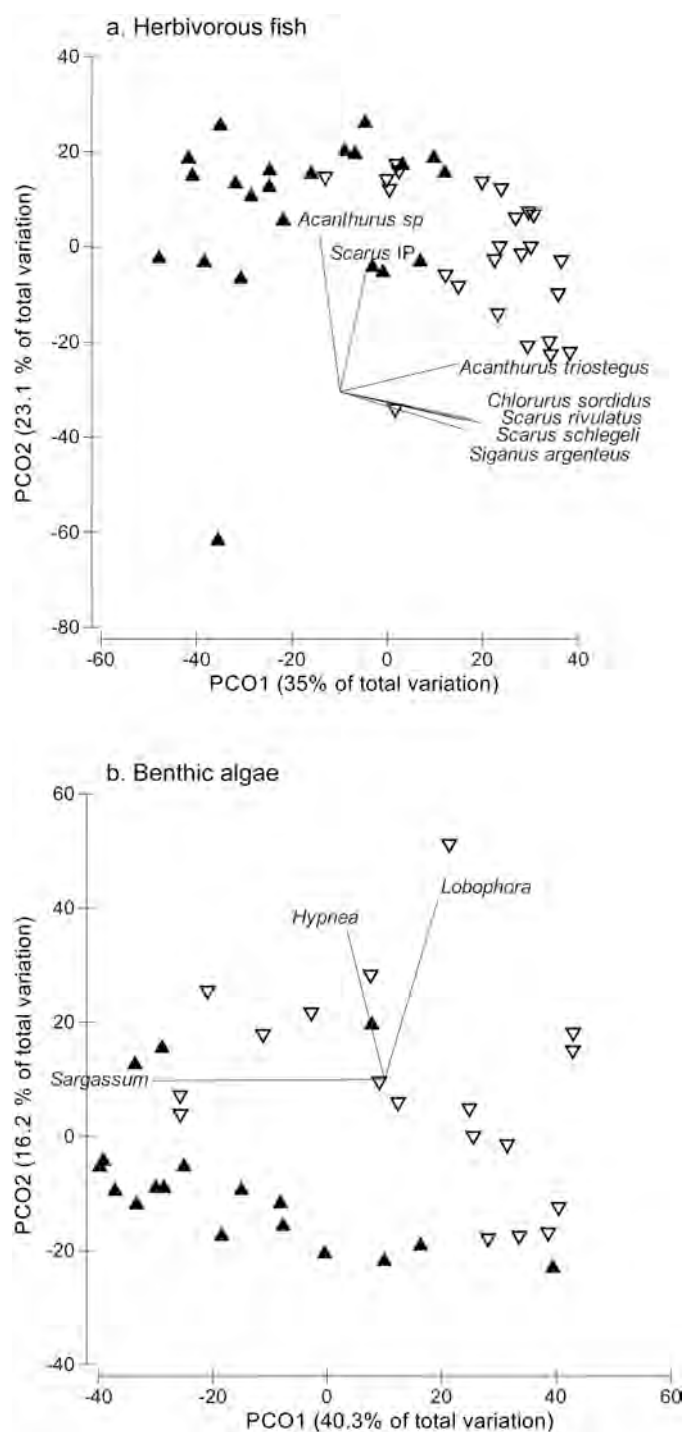


Figure 6.2. Principal coordinate analysis comparing (a) herbivorous fish and (b) benthic algae community composition from lagoon and reef-flat habitats at Ningaloo Reef. Herbivorous fish data were log (x+1) transformed and benthic algae data were fourth root transformed prior to analysis. Upward facing solid triangles = lagoon; downward facing triangles hollow triangles = reef flat. Vector overlays represent correlations > 0.6 based on Spearman ranking.

2011

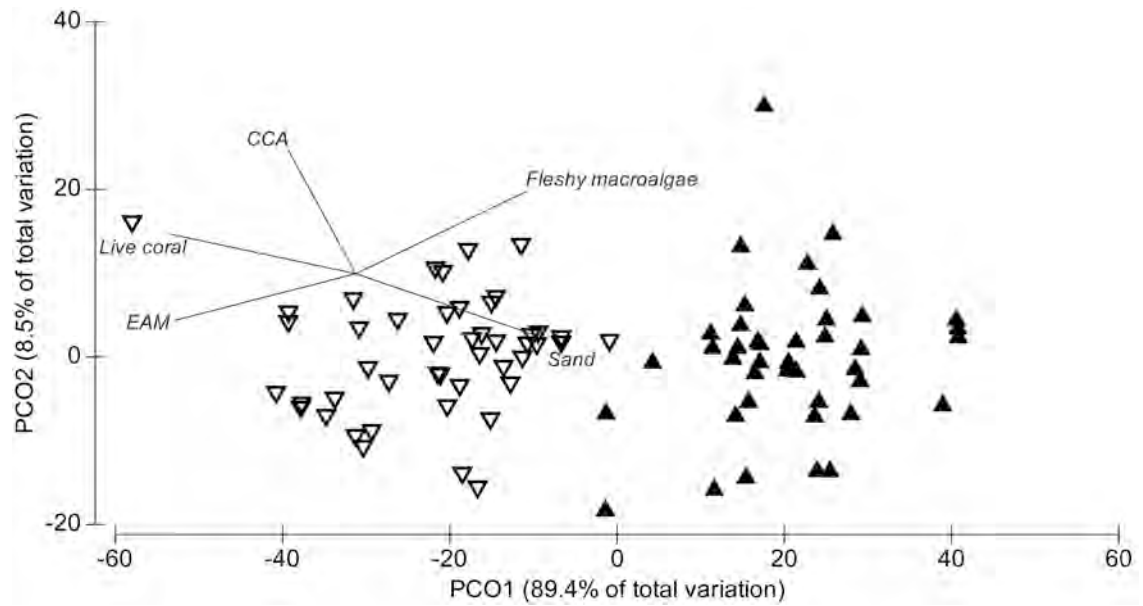


Figure 6.3. Principal coordinate analysis comparing benthic community composition (% cover) from lagoon and reef-flat habitats. Data were $\sin(\sqrt{x})$ transformed prior to analysis. Upward facing solid triangles = lagoon; downward facing triangles hollow triangles = reef flat. CCA = crustose coralline algae. EAM = Epilithic algal matrix. Vector overlays represent correlations > 0.6 based on Spearman ranking.

2011

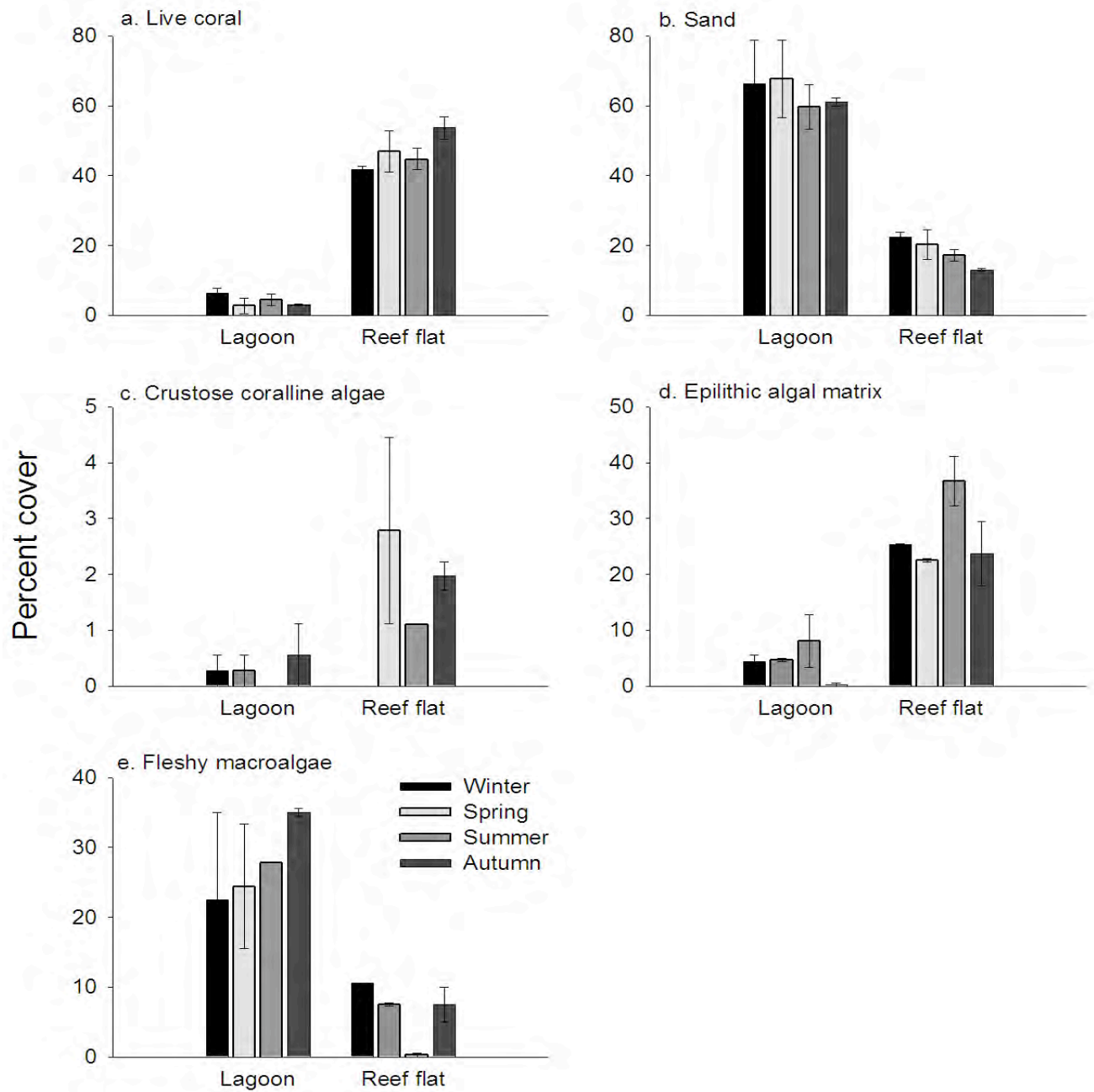


Figure 6.4. Mean cover (% \pm SE) of (a) live coral, (b) sand, (c) crustose coralline algae, (d) epilithic algal matrix, and (e) fleshy macroalgae in lagoon and reef-flat habitats during winter, spring, summer, and autumn, at Ningaloo Reef. Note the different scales on the y axes for each functional group.

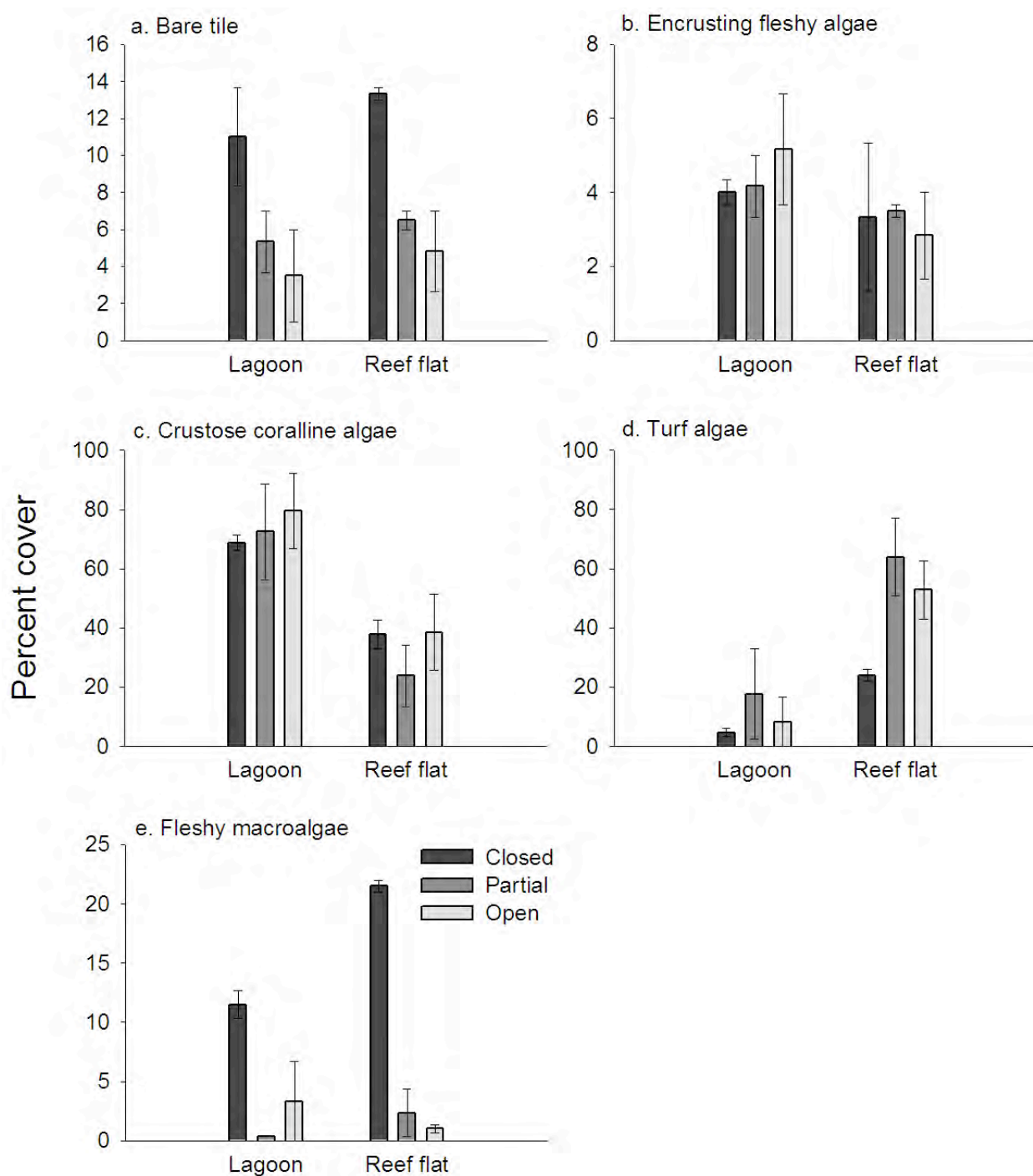


Figure 6.5. Mean cover ($\% \pm SE$) of different functional groups after six months on the topside of recruitment tiles in lagoon and reef-flat habitats depending on herbivore exclusion treatments. Note the different scales on the y axes for each functional group. Closed = herbivores excluded; Partial cage = cage with lid and one side only; Open = no cage.

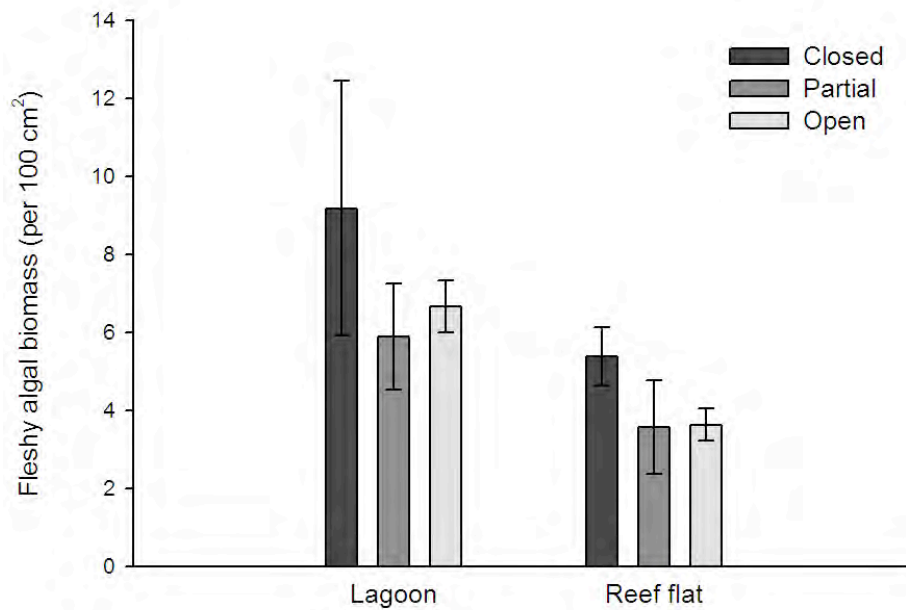


Figure 6.6. Mean biomass (mg \pm SE per 100 cm²) of fleshy algae on recruitment tiles after six months in lagoon and reef-flat habitats depending on herbivore exclusion treatments. Closed = herbivores excluded; Partial cage = cage with lid and one side only; Open = no cage.

Discussion

Distinct patterns in the benthic algal and herbivorous fish communities were observed between adjacent lagoon and reef-flat habitats at Ningaloo Reef over a full seasonal cycle. Ningaloo Reef is a relatively pristine fringing coral-reef ecosystem that is dominated by high coral cover and abundant herbivorous fish communities, and algal recruitment dynamics were strongly influenced by herbivory in both lagoon and reef-flat habitats. In both habitats, herbivory equally limited the recruiting algal community, but differences between algal functional groups were influenced at a localised scale. At a broader spatial scale, large fleshy macroalgae were seasonally more abundant in the lagoon where the herbivorous fish community was characterised by fewer and smaller individuals. On the contrary, high coral cover dominated the reef flat, providing structure for an abundant and diverse herbivorous fish community that limited fleshy macroalgal abundance via herbivory and reduced settlement space for algal recruits (Williams et al. 2001, Bejarano et al. 2011, Vergés et al. Chapter 2).

Patterns in the spatial distribution of benthic coral-reef algae are determined by different levels of grazing, nutrient inputs, substrate availability, hydrodynamics, and recruitment (Lubchenco & Gaines 1981, Santelices 1990). In our study, we have clearly demonstrated that patterns of the spatial distribution of recruiting fleshy algae were influenced by patterns of herbivory and space availability. When recruitment space was equal in the lagoon and reef-flat habitats, herbivory was an important mechanism that influenced the abundance of fleshy macroalgae on the recruitment tiles. Both the cover and biomass of fleshy macroalgae were significantly higher in the herbivore exclusion treatments, yet there were no differences in the biomass of the algae between the two habitats. Similarly, recent evidence also demonstrated that the biomass of adult *Lobophora variegata* was the same in the lagoon and reef-flat habitats when herbivores were excluded for 6 weeks from the algae at Ningaloo Reef (Vergés et al. Chapter 2). This suggests that both the input of algal propagules and algal productivity in both habitats were similar during the time of our study.

In contrast to the biomass of the caged recruiting fleshy macroalgae in this study, there was no difference in the algal cover or biomass between the lagoon and reef-flat habitats when herbivores were allowed access to graze the recruitment tiles. The abundance of herbivores was relatively low in the lagoon compared to the reef flat; yet, the herbivore community found in the lagoon habitat nevertheless strongly influenced the recruiting macroalgal community. Therefore, we suggest that there were no recruitment or nutrient limitations on early algal cover and growth when space availability was unlimited. Similar to other recruitment studies that have identified the roving herbivores in limiting the abundance of fleshy macroalgae (Belliveau & Paul 2002, Diaz-Pulido & McCook 2003, Burkepile & Hay 2006, Albert et al. 2008), herbivory was an important post recruitment process driving early algal community structure in this coral-reef ecosystem.

While roving herbivorous fish affected the cover and biomass of fleshy macroalgae, apparent differences in the community composition of the algal recruits between the lagoon and reef flat was influenced by the presence of territorial damselfish at a local scale. In our study, damselfish were present at some of the treatments within the reef-flat sites where they tended to increase the amount of turf and decrease the amount of CCA cover. They were never found in the lagoon where turf algal cover was relatively low and CCA cover was relatively high, and they did not affect the amount of fleshy macroalgae cover or biomass in either habitat. Other studies have demonstrated that large roving herbivores have a significant influence on the broad benthic algal community structure (Mumby et al. 2006, Paddock et al. 2006, Fox & Bellwood 2007, Wismer et al. 2009, Vergés et al. Chapter 2), while the farming practices of territorial damselfish can instead influence turf productivity and diversity at smaller scales (Klumpp et al. 1987, Ceccarelli et al. 2005, Gobler et al. 2006, Hoey & Bellwood 2010c). Territorial damselfish often chase away larger roving herbivores to protect the turf algal communities that they farm, influencing patterns of algal recruitment and

succession (Hixon & Brostoff 1996, Ceccarelli et al. 2001, Ceccarelli et al. 2006). Although we did not quantify their effect on the standing algal community, the presence of territorial damselfish in the reef-flat sites presumably influenced the high EAM cover in the reef flat. These patches add to the spatial heterogeneity of algae in a coral-dominated reef habitats, providing an important source of nutrition to meso- and macro-herbivores (Smith et al. 2001, Wilson et al. 2003).

Distinct differences between the benthic algal communities were observed in the lagoon and reef-flat habitats, yet these differences were not reflected in the algal biomass and cover which were seasonally dependent. The lagoon and reef flat had a similar cover and biomass of fleshy macroalgae through the year, except for autumn when the lagoon was characterised by a dramatic increase in macroalgae. Similar to studies from the Great Barrier Reef (GBR) that found seasonal increases in algal cover in autumn (Schaffelke & Klumpp 1997, Lefevre & Bellwood 2010), the increase of macroalgae found in the lagoon at Ningaloo Reef was dominated by *Sargassum*. Although we do not exclude the influence of nutrients or phenology on algal abundance, the difference in macroalgal cover between the lagoon and reef-flat habitats at Ningaloo Reef appears to be highly influenced by the characteristics of the herbivorous fish community in both habitats.

In the present study, while the herbivore community found in the lagoon habitat influenced the recruiting fleshy algal abundance, it was obviously not able to limit seasonal increases in *Sargassum*. While we did not directly test whether herbivory was controlling the benthic algal abundance in our study, it was recently demonstrated that both *Sargassum myriocystum* and *Lobophora variegata* were heavily consumed by grazers in the reef-flat habitat at Ningaloo Reef, but that herbivores did not consume these algae in the lagoon due to the lack of large browsers (Vergés et al. Chapter 2). Although herbivory is not uniform, roving herbivorous fish are known to significantly limit the growth and density of both *Sargassum* and *Lobophora* recruits (Diaz-Pulido & McCook 2003). Thus, we suggest that the algae may have a certain size, abundance, or seasonal increase in productivity where they are able to escape consumption by the grazers found in the lagoon at Ningaloo Reef due to their low biomass in that habitat. On the contrary, the abundance and diversity of the grazer community found in the reef-flat habitat appears enough to limit macroalgal growth throughout the year. Although their biomasses were low, *Lobophora variegata* and *Dictyota* sp. were characteristic the macroalgae found on the reef flat. Compared to *Sargassum*, these macroalgae are not highly palatable to large herbivores (Steinberg & Paul 1990, Mumby et al. 2005, Bittick et al. 2010), and this may explain their dominance where herbivory is high. Thus, we find that herbivore abundance and diversity influenced both the abundance and community composition of macroalgae found in the lagoon and reef-flat habitats.

In general, many studies have demonstrated that tropical algal distribution is highly influenced by different levels of herbivory (Burkepile & Hay 2006) from echinoids in Caribbean reefs (Sammarco 1982, Edmunds & Carpenter 2001) to both roving and territorial fish in most reefs (Klumpp & McKinnon 1992, McClanahan 1997, Ceccarelli et al. 2001, Bellwood et al. 2004, Hughes et al. 2007, Wismer et al. 2009, Vergés et al. Chapter 2). There is an abundant and diverse community of herbivorous fish at Ningaloo Reef dominated by fish from each major functional group (Green & Bellwood 2009), similar to abundances found in offshore reefs on the GBR (Wismer et al. 2009). Diverse guilds of herbivores are necessary for resilience on coral reefs (Bellwood et al. 2004, Cheal et al. 2010, Hughes et al. 2010), and their abundance and diversity at Ningaloo Reef suggests that they support the resilience of this unique fringing coral-reef ecosystem by limiting algal recruitment. While there were no seasonal changes to the fish community, the abundance of palatable macroalgae in lagoon habitats at Ningaloo Reef did alter seasonally, yet this was not found in adjacent reef-flat habitats characterised by live coral. Coral reefs are spatial mosaics of different habitats, which host a diversity of flora and fauna, and the fish and algal communities at Ningaloo Reef offer complexity to distinct habitats within small spatial scales that connect this extensive fringing coral reef.

CHAPTER 7. Main findings and outcomes

The consumption of macrophytes by herbivores is a particularly important ecological process in coral reefs that supports intricate food webs and strongly contributes to the resilience of these systems following disturbances such as cyclones or bleaching events (Bellwood et al. 2004; Mumby et al. 2006). Broadly, this project aimed to characterise plant-herbivore interactions in the Ningaloo Reef Marine Park, and has provided the first quantification of the process of herbivory in this region. In doing so, it has provided key information to answer the management questions identified in the Ningaloo Research Program Research Priorities. The questions relevant to this study are:

1. What is the species diversity of key flora and fauna in selected representative habitats?
2. What is the abundance, size composition and distribution of these key species?
3. Do variations in predator abundance indirectly affect reef ecosystem structure including the abundance of grazers, algae and corals and corallivorous gastropods (*Drupella*)?
4. Are current management arrangements/regulations appropriate for preserving the biodiversity represented within the park?

The following provides the key findings and relevant management implications under the headings of the management questions.

What is the species diversity of key flora and fauna in selected representative habitats, and what is the abundance, size composition and distribution of these key species?

The biomass and species composition of roving herbivorous fishes varied among the five regions examined (Bundegi, Mandu, Point Cloates, Maud and Gnaraloo) using underwater visual censuses. Using underwater video cameras, 23 different fish species were observed consuming macroalgae, but seven species (*Naso unicornis*, *Kyphosus* sp., *K. vaigiensis*, *Siganus doliatus*, *Scarus ghobban*, *S. schlegeli* and initial-phase *Scarus* sp.) together accounted for 95% of the observed bites across five regions. Of these species, three taxa were identified as the most important in consuming macroalgal (*Sargassum myriocystum*) assays: *N. unicornis*, *Kyphosus* sp. and *K. vaigiensis*. These results were supported by stable isotope analyses that incorporate nutrients from food sources over far longer periods than those examined using the assay approach.

The structurally complex coral-dominated outer reef and reef-flat habitats were characterised by the highest biomass of herbivorous fish and greatest levels of herbivory (based on *Sargassum* assays), compared to lagoon habitat. There was also a high degree of variability in grazing rates among regions separated by hundred of kilometers in the marine park, with different species responsible for macroalgal removal among those regions.

A transcontinental comparison between Keppel Islands in the Great Barrier Reef (GBR) on the east coast of Australia and Ningaloo Reef, showed differences in the diversity of the species observed feeding and the species composition of roving herbivorous fishes between the two continental regions. In Ningaloo Reef, 23 species were observed biting on *Sargassum*, compared with just 8 in the Keppel Islands. The larger number of species feeding on macroalgae in Ningaloo Reef suggests that there may be higher functional redundancy among macroalgal consumers in this system, however, a large proportion of herbivory was dependent on only a few species in both regions.

Management implications and recommendations:

- We have provided a baseline survey of all nominally herbivorous fish species (fish density and quantitative feeding activity data) across a range of regions and we have identified key species that should be closely monitored.
- We provide evidence that structural complexity is a key factor influencing herbivory. Conservation efforts should thus focus on conserving this trait (e.g. protect coral habitats from anchoring damage).
- Although herbivorous fishes are not presently targeted by fishers in NMP, this trophic group is increasingly being targeted for exploitation elsewhere. We have provided quantitative data that can be used to support potential management plans aimed at protecting herbivorous fishes from exploitation on the basis of their critical role for promoting coral-reef resilience.
- A direct comparison of herbivory between different coral-reef systems, indicates that Ningaloo Reef is a comparatively pristine system.

Do variations in predator abundance indirectly affect reef ecosystem structure including the abundance of grazers, algae and corals and corallivorous gastropods (*Drupella*)?

Collectively, *N. unicornis*, *Kyphosus* sp. and *K. vaigiensis* accounted for only 1-7% of roving herbivorous fish biomass across regions, yet were responsible for 85-99% of the bite rates on *Sargassum* being quantified in these regions (except in Mandu, where browsers were depauperate). Rates of herbivory could not be predicted based on the distribution of macroalgal browsers in each region.

There were high levels of variability in the importance of different food sources across both habitats and regions for some consumers (e.g. *Siganus* spp.), but consistency for other species (e.g. *Naso unicornis*, *Kyphosus* spp.), which is likely to reflect shifts in food source availability or feeding preferences.

Herbivory had an equally strong effect on the community composition of algal recruits in the lagoon and reef-flat habitats, despite the reef flat hosting a herbivorous fish community that is an order of magnitude greater in terms of biomass than the lagoon, which is characterised by younger and smaller fish (e.g. *Scarus* initial phase). Differences among habitats in algal biomass were strongly influenced by season. Lagoon habitats only have higher biomass than reef flat habitats during part of the year (late summer/ early autumn). Apparent habitat differences in community composition of algal recruits were in fact driven by the presence of damselfish, which were only present in some of the treatments within the reef-flat (but never in the lagoon).

Management implications and recommendations:

- Variability in grazing rates across NMP, and the species responsible for grazing, indicates that any future monitoring of key species needs to take place over different regions of the marine park.
- Herbivory is a dominant mechanism that influences the abundance of fleshy macroalgae when recruitment space is equal in the lagoon and reef-flat habitats. Zoning needs to consider the movement of key herbivores across habitats when determining boundaries of management zones.

Are current management arrangements/regulations appropriate for preserving the biodiversity represented within the park?

Other Node 3.2.2 sub-projects showed no differences in algae or corals between Sanctuary and Recreational zones, suggesting no apparent cascading trophic effects on benthic organisms in NMP. Interestingly, those studies also showed higher grazer biomass in sanctuary zones, particularly in relation to parrotfishes. Our results indicate that total grazer biomass as a poor indicator of potential grazing, and its use in implying trophic effects could lead to erroneous conclusions. Only a few of the 23 roving herbivorous species play a significant role in macroalgal removal.

Other Node 3.2.2 sub-projects have shown that the herbivore *Kyphosus sydneyanus* moves between lagoon and reef-slope habitats, but are likely to remain within a region. Our study has shown the importance of kyphosid species in removing macroalgae, but there is variability in their abundances across regions. Furthermore, *N. unicornis* is an important species for the removal of macroalgae. While these herbivore species are not targeted by fishers, they are likely to be susceptible to changes in the abundances of higher order predators such as sharks, which have been shown in other Node 3.2.2 sub-projects to be affected by fishing activities leading to potential trophic cascades. Furthermore, these grazers are also likely to be susceptible to non-fishing human disturbances (e.g. oil spills and coral damage) and natural disturbances that affect coral structure (e.g. cyclones).

Management implications and recommendations:

- Monitoring the biomass of *Naso unicornis*, *Kyphosus* spp. inside and outside sanctuary zones will provide crucial information of the potential influence of zoning on macroalgal removal in the NMP, as well as a region's ability to recover from disturbances that enhance macroalgal production.
- Quantitative data on rates of herbivory from our studies can be incorporated into broad-scale fish density data from other projects to model the effects of disturbances and changes in management strategies on herbivory, and potential effects to the system as a whole.
- Data on the spatial patterns of movement are needed for all key macroalgal grazers to ensure that sanctuary zones preserve their abundances.
- Research is needed to further investigate the potential for indirect ecological effects and trophic cascades through the removal of higher order predators (e.g. sharks) in the NMP.

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Publications

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